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17TH SOUTHERN FOREST TREE IMPROVEMENT CONFERENCE

June 6-9, 1983
University of Georgia

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The Southern Forest Tree Improvement Committee

PROCEEDINGS OF THE
SEVENTEENTH SOUTHERN FOREST TREE IMPROVEMENT CONFERENCE

June 7-9, 1983

The University of Georgia

Athens, Georgia

Sponsored Publication No. 39 of the

Southern Forest Tree Improvement Committee

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FOREWORD

The Seventeenth Southern Forest Tree Improvement Conference was held at the Georgia Center for Continuing Education on the campus of the University of Georgia at Athens, Georgia. Co-sponsors were the School of Forest Resources of the University of Georgia and the Southeastern Forest Experiment Station, U.S. Department of Agriculture, Forest Service.

Registered for the meeting were 203 attendees representing 24 states and 3 foreign countries. Eight invited papers and 32 offered papers were presented during the three-day conference in eight technical sessions: Tree Breeding in International Forestry; Advances in Seed Orchard Management; Selection and Breeding Strategies; Progeny Testing Methodology; Variation, Heritability and Gain in Hardwoods; Variation, Heritability and Gain in Conifers; and Accelerated Breeding and Early Selection.

At the Twelfth SFTIC in 1973, a survey was taken to assess the nature and urgency of problems facing tree improvement in the South. A summary of this survey was presented in the Conference proceedings. The SFTIC chose to repeat this survey after 10 years at the Seventeenth SFTIC and the results are presented in the section entitled, "Southern Forest Tree Improvement Problems and Research Priorities" at the end of these proceedings.

The proceedings also contain a history of the Southern Forest Tree Improvement Conference 1971-1981 by A. E. Squillace. This history supplements the earlier treatise by C. M. Kaufman in 1971 and completes the SFTIC history from its beginning in 1951 through 1981.

Conference Co-Chairmen:
Dr. Bruce C. Bongarten
School of Forest Resources
University of Georgia
Athens, Georgia 30602

Dr. Harry O. Yates, III
Southeastern Forest Experiment Station
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SOUTHERN FOREST TREE IMPROVEMENT

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June 9, 1983

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CONTENTS

Page

KEYNOTE ADDRESS

Forest Genetics - The U.S. Contribution to National Forestry - The Federal Role
Stanley L. Krugman........ 1

TREE BREEDING IN INTERNATIONAL FORESTRY

Ten Years of Industrial Tree Improvement in Columbia (invited paper)
William E. Ladrach........ 8

Strategy for the Development of Conservation Banks and Breeding Programs for Coniferous Species from Central America and Mexico
William S. Dvorak........ 22

PINUS CARIBAEA Cone Maturation in Puerto Rico
Clark W. Lantz........ 30

New Directions and Problems for Tree Breeding in the Tropics (invited paper)
Jeffery Burley........ 34

ADVANCES IN SEED ORCHARD MANAGEMENT

Geographic Location Affects Flowering of Loblolly Pines
R.C. Schmidtling........ 42

Third-Year Seed Production in Outplanted Sweetgum Related to Nursery Root Colonization by Endomycorrhizal Fungi
Paul P. Kormanik........ 49

Pine Wilt and Pitch Canker of Virginia Pine in Seed Orchards
L. David Dwinell and Jane Barrows-Broaddus........ 55

Cytex and Other Chemicals Effectively Inhibit Conelet Abortion in Longleaf Pine
Robert C. Hare........ 63

Measuring Pollen Contamination in Clonal Seed Orchards with the Aid of Genetic Markers
D.B. Smith and W.T. Adams........ 69

Feasibility of Supplemental Mass Pollination to Increase Genetic Gains from Seed Orchards
F.E. Bridgwater and C.G. Williams........ 78

Pollination Success in Relation to Female Flower Development in Loblolly Pine
David L. Bramlett and Frederick R. Matthews........ 84

SELECTION AND BREEDING STRATEGIES

A Tree Improvement Program for Southern Hardwoods
R.C. Purnell and R.C. Kellison.................................. 90

Economic Benefits of an Aggressive Breeding Program
S.E. McKeand and R.J. Weir...................................... 99

Low Level Inbreeding Effects on Germination, Survival, and Early Height Growth of Slash Pine
P.A. Layton and R.E. Goddard.................................... 106

The Question of Genetic Management of Minor or Undomesticated Species - An Outsider's Reaction
R.D. Burdon... 116

Crown-Quality Assessment and the Relative Economic Importance of Growth and Crown Characters in Mature Loblolly Pine
Cheryl L. Busby... 121

Concepts for Analysis of Intergenotypic Competition in Forest Trees
Warren L. Nance, S.B. Land, Jr., and Richard F. Daniels......... 131

A Multiple-Objective Forest Tree Breeding Strategy
Samuel B. Land, Jr. and T.H. Mattheiss.......................... 146

PORGENY TESTING METHODOLOGY

Lessons from One Generation of Progeny Testing (invited paper)
Robert J. Weir, J.P. van Buijtenen, and R.E. Goddard............ 157

Progeny Test Design and Analysis (invited paper)
J.P. van Buijtenen.. 161

Use of a Lattice Square Design to Evaluate Family Effects: Accounting for Environmental Variation
Stuart E. Duba, John A. McGuire, and James F. Goggans........... 171

Alternative Designs for Progeny Testing Slash Pine
Donald L. Rockwood.. 179

Growth of Tissue Culture Plantlets of Loblolly Pine in a Nursery and Greenhouse
L.A. Wisniewski, S.E. McKeand, and R.E. Brooks.................. 186

Performance of Single Family Versus Mixed Family Plantation Blocks of Loblolly Pine
C.G. Williams, F.E. Bridgwater, and C.C. Lambeth................ 194

VARIATION, HERITABILITY AND GAIN IN HARDWOODS

Variation and Heritability of Branching and Growth Characteristics Among Sycamore Progeny
Charles J. Jourdain and James R. Olson.......................... 203

VARIATION, HERITABILITY AND GAIN IN HARDWOODS (continued)

Estimation of Gain in Form, Quality and Volumetric Traits of American Sycamore in Response to the Selection for Tree Dry Weight
Barbara G. McCutchan.. 209

Genetic Variation of Six-Year-Old Open-Pollinated Progeny of Sweet Pecan Trees
John R. Toliver and Furcy J. Zeringue.......................... 220

Geographic Variability in Growth of Ten-Year-Old Green Ash Families Within East Texas
A.F. Stauder, III and W.J. Lowe................................ 227

Geographic Patterns of Variation Among Sweetgum Populations in the Southern United States - Fourteenth-Year Results
George W. Stubblefield... 234

VARIATION, HERITABILITY AND GAIN IN CONIFERS

Fifth Year Performance of Wide Ranging Loblolly Pine Provenances
John A. Pait, III and Lee Draper, Jr........................... 245

Three Increments of Gain from Three Stages of Selection in Slash and Longleaf Pines and Heritabilities at Age 21 Years
Earl R. Sluder... 253

Relation Between Height Growth and Fusiform Rust Infection in Slash Pine
A.E. Squillace, P.A. Layton, and R.E. Goddard.................. 262

Operational Plantations of Improved Slash Pine: Age 15 Results
Larry Tankersley, Bruce Bongarten, Graham Brister, and Marvin Zoerb.. 271

Genetic Variation of Cones, Seeds, and Nursery-Grown Seedlings of Baldcypress (_Taxodium distichum_ (L.) Rich.) Provenances
Stephen Faulkner and John Toliver.............................. 281

ACCELERATED BREEDING AND EARLY SELECTION

Maximizing Genetic Gain in Loblolly Pine by Application of Accelerated Breeding Methods and New Concepts in Orchard Design (invited paper)
Michael S. Greenwood... 290

Early Testing - An Overview with Emphasis on Loblolly Pine
Clements C. Lambeth.. 297

Biochemical Methods for Accelerating Progress in Tree Improvement (invited paper)
James W. Hanover... 312

Potential of _IN VITRO_ Screening of Loblolly Pine for Fusiform Rust Resistance
L.J. Frampton, Jr., H.V. Amerson, and R.J. Weir................ 325

ACCELERATED BREEDING AND EARLY SELECTION (continued)

Patterns of Genetic and Environmental Variance in a Short-Term Progeny Test of Loblolly Pine
E.C. Franklin.......... 332

POSTER SESSION ABSTRACTS

Increase and Spread of Brown Spot Needle Blight Within Single and Multiple Family Plantings of Open-Pollinated Longlead Pine
Margene M. Griggs.......... 345

A Trial to Mechanically Sort Clones from a Bulk Seed Lot
Robert P. Karrfalt.......... 346

Forest Crop Improvement by Tissue Culture
R.L. Mott and H.V. Amerson.......... 347

Population Genetic Structure of the Douglas-Fir Shelterwood Regeneration System in Southwest Oregon
David Neale.......... 348

Adventitious Shott Formation on Embryos of *Pinus Palustris* Mill., *P. Elliottii* Engelm. and *P. Palustris* x *Elliottii*
Michael Stine and Harry E. Sommer.......... 349

In Vitro Propagation of *Liquidambar Styraciflua* L.
Harry E. Sommer, Hazel Y. Wetzstein, and Ni Lee.......... 351

Wide Crosses to Improve Fusiform Rust Resistance in Slash Pine
C.H. Walkinshaw and M.M. Griggs.......... 352

Geographic Variation in Loblolly Pine
O.O. Wells.......... 353

HISTORY OF S.F.T.I.C. AND RESEARCH PRIORITIES QUESTIONAIRE

Southern Forest Tree Improvement Problems and Research Priorities - June 1983
O.O. Wells, David Bramlett, and Susan Kossuth.......... 355

The Southern Forest Tree Improvement Committee, 1971-81
A.E. Squillace.......... 359

FOREST GENETICS - THE U.S. CONTRIBUTION TO INTERNATIONAL FORESTRY - THE FEDERAL ROLE

Stanley L. Krugman[1]

Abstract--Following World War II, the U.S. Government began a major program to reduce hunger and malnutrition in many countries. Their effort became known as the Food for Peace Program. Funds from this effort led to a special research program in over 50 countries. As part of this effort forest geneticists from both the U.S. and 30 countries initiated joint research in flowering physiology and vegetative propagation, seed orchard management, breeding, species introduction trials, and studies in quantitative genetics. Currently forest genetics studies are still underway in 5 countries supported by the Special Foreign Currency Research Program.

In the last 15 years, forestry has played a more important role in the foreign policy of the United States. Through such State Department agencies as Agency for International Development (AID), major forestry schemes have been developed. In support of these forestry development efforts, modest research and development programs have been initiated in forest genetics in over 35 countries. For the most part these have included the initiation of species tests and the training of foreign forest geneticists. These efforts are currently supported by Science and Technology agreements between the U.S. and the other nations.

The more active genetic programs that I am directly involved with include: those in Egypt--trees for windbreak and shelterbelts as well as roundwood; Spain--the establishment of a national genetics program; People's Republic of China--initiation of species tests and germplasm exchanges; Yugoslavia--joint studies in breeding; India--the development of fast-growing hybrids; and Pakistan--species tests for arid lands.

New exchanges are in the planning stages with Chile, France, and Australia.

As forestry becomes more important in our foreign aid programs, I see forest genetics as a major effort in support of these programs.

Additional keywords: Foreign forestry, science and technology exchanges, germplasm exchanges.

---

[1] Director, Timber Management Research, USDA Forest Service, Washington, D.C.

INTRODUCTION

USDA Forest Service research has had a modest international role for over 80 years. Initially most of this international involvement was in the area of forest products and international trade. It was not until after World War II that Forest Service genetics and tree improvement activities became involved in the international scene.

The major stimulation for this activity was the Special Foreign Currency Research Program, better known as the Food for Peace Program, or the Public Law 480 Program. Following World War II, the U.S. Government began a program to reduce worldwide hunger and malnutrition. Countries repayed the U.S. in their own currencies and most of the repayments remained in the host countries. These funds were then used to improve their quality of life, i.e., to build schools, roads, hospitals, and to support research. As part of this research effort forest geneticists and associated reseachers initiated joint research in over 30 countries. Studies included flowering physiology, vegetative propagation, seed orchard management, breeding, hybridization, population studies, tissue culture, and terpene analysis. Most of these studies were completed by the late 1960s as the funds were no longer available or devoted to other uses.

The completed studies in Columbia, Chile, Brazil, and Uruguay were involved with the evaluation of physiology of slash (Pinus elliottii, Engelm.) and loblolly pine (Pinus taeda L.). These studies included seed source studies in the individual countries as well as flowering physiology and tissue culture investigations. Studies in Columbia explored grafting using different root stock and scion combinations. Flowering was also carefully studied since flowering of these species become erratic in the tropics. Results have been published in both internal reports and scientific publications. In Columbia, one investigation was directed to the haploid culture of pines, mostly with sugar pine (Pinus lambertiana Dougl.).

Table 1 summarizes the countries and the number of major genetic or related studies that we have conducted. In this brief paper, I will attempt only to provide a summary of our activities, since time does not allow a more detailed discussion. However, much of the results of these earlier studies have been published, although often in foreign journals.

Table 1. Countries in which major forest, genetics and related projects were supported by PL-480 funding

Country	Number of Projects	Country	Number of Projects
Brazil	1	Pakistan	16
Chile	3	Peru	1
Columbia	2	Poland	15
Egypt	3	Spain	3
Finland	12	Sri Lanka	2
Greece	3	Taiwan	1
India	17	Tunisia	1
Israel	3	Uruguay	1
Italy	3	Yugoslavia	10
Korea	1		

Currently, PL-480 forestry research is only funded in India and Pakistan. The major active studies in Pakistan include superior selection studies of poplar clones, provenance trials with Himalayan blue pine (*Pinus wallichiana* A. B. Jacks), screening trees and woody shrubs for the arid zones, and the preparation of a monograph on *Eucalyptus camaldulensis* Dehn, *E. microthea* F.v.M. and *E. tereticornis* Sm. We are also supporting a number of related programs including management of improved poplar selections and a modest program of selecting species for windbreaks. In India, our major genetic studies deal with the tree improvement in *Eucalyptus tereticornis*.

In many of the developing countries, there is research underway in forest genetics but usually such research is rarely published. We have used Special Currency Funds to a limited extent to get these data organized and published. Such is the case with the above monograph on *Eucalyptus* from Pakistan.

Because of the frequency of requests for information on arid land species and because there is relatively little research in the U.S. in this area, we have encouraged considerable arid land research under the PL-480 program. For example, in Pakistan we are screening at nine sites 62 species from 22 genera under semi-arid conditions. The designs are simple but the results have been most promising. Such research most likely would not have been done by the more traditional methods of funding by the host countries. If the situation permits, I establish essentially similar studies in other countries in an effort to screen the same germplasm in as many environments as possible.

Our foreign programs have often taken us in strange directions. We are currently completing a PL-480 genetics program with Egypt. The main aim of this investigation was the identification and screening of tree species for windbreaks and shelterbelts. This has led to the development of a number of linear plantations and the establishment of a small private particle-board plant. We have collected across North Africa and the middle East one of the finest collections of Eucalyptus camaldulensis, and recently completed a collection of Casuarina. In Egypt, we are also screening for tolerance to an array of soil conditions and already we have detected several promising seed sources of Eucalyptus camaldulensis for salt conditions. This modest project has demonstrated the feasibility of planting trees for an array of uses in the Egyptian western desert in conjunction with their agricultural projects.

BILATERAL AGREEMENTS

With the passing of the PL-480 programs, the U.S. has initiated bilateral research agreements with several countries. With Israel, we are currently conducting Eucalyptus propagation studies. With Yugoslavia, we are continuing a joint investigation on the incompatibility systems between European Black Pine (Pinus nigra Arnold) and Scots pine (Pinus sylvestris L.) and the means for mass production of this hybrid. In Poland, we have an excellent joint study on the genetic basis for forest tree resistance to toxic gases. Flowering physiology studies have been underway in Poland for over 15 years and one of these is still being supported. Like the PL-480 funding, funds for these projects are very limited, and we can expect fewer projects.

AID RELATED PROJECTS

In the last 15 years forestry has started to play a more important role in the foreign policy of the United States. Through such State Department agencies as the U.S. Agency for International Development (AID), major forestry schemes have been developed and funded. Many of these programs deal with reforestation and fuel wood production. In support of these activities, modest research and development programs have been initiated in forest genetics or tree improvement in 35 countries. For the most part these projects have included germplasm collections, species tests, and seed production. In a few cases, the projects have involved training geneticists. Currently, we are screening approximately 210 species from 50 genera. In addition, we are assisting in the development of forest tree germplasm conservation programs in at least 15 countries. These efforts are currently requested and supported by various Science and Technology agreements between the U.S. and the other nations.

SCIENCE AND TECHNOLOGY EXCHANGES

In addition to the above projects, USDA, thru its Office of International Cooperation and Development (OICD), supports several scientific exchanges in forest genetics. Recently a 6-year research project with Spain was completed under this program. In the course of this project, 15 forest tree species and 192 seed sources were planted in 32 locations in northern Spain. Although the project has officially ended, we will continue our cooperation since these test plantings have yet to be evaluated.

We did conduct a major meeting in Spain on the science of species introductions which will be published later this year in several different languages.

The species now being tested in Spain are summarized in Table 2. The results of this type of investigation will have application outside of Spain.

Table 2. Major tree species being introduced into Spain under the OICD program

Species	Number of Seed Sources	Locations
Abies concolor (Gord. and Glend.) Lindl.	1	1
Libocedrus decurrens Torr.	1	1
Pinus contorta Engelm.	23	5
Pinus jeffreyi Grev. and Bulf.	4	2
Pinus ponderosa Laws	2	1
Prunus serotina Ehrh.	22	5
Pseudotsuga menziesii (Murb.) Franco	87	18
Sequoia sempervirens (D. Don) Endl.	5	3

Other Science and Technology genetic research projects have also been initiated in the past with several Eastern Bloc countries. Although the program with the USSR is officially over, we are still conducting annual exchanges of germplasm. From the USSR, we have obtained excellent collections of Scots pine and white elm (Ulmus pumila L.) as well as a large number of new collections of cold hardy material from eastern USSR. At this time, we have one active field study of U.S. species underway in the southern parts of the USSR where we have established six test locations.

During the last three years, we have also initiated a series of studies with the People's Republic of China. Our first major effort will be a loblolly and slash pine seed source studies in eastern China (Figure 1). Within the next two years, we are planning a Paulownia test of at least five species in the United States.

We have received small quantities of seed of 210 species representing 81 genera from China for distribution in the U.S. as well as to other countries; and this material has been provided to over 60 cooperators in the U.S. New cooperative programs are in the planning stages with Chile, France, West Germany, and Australia. With both Chile and Australia, we hope to develop better mechanisms for germplasm collections and exchanges. We have also exchanged scientists and plant material with France and have initiated several hardwood genetic studies with red oak, walnut, and black cherry.

CONCLUSION

As forestry becomes more important in our foreign aid program, I see a larger role for forest genetics. In most countries the main problems are associated with limited resource and major reforestation needs. There are many contributions that we as forest geneticists can make, and I hope that those of you who are interested will join us in these activities. We plan to continue to use these foreign research opportunities to further our knowledge of our own species as well as exotics. I feel strongly that when such programs are properly designed, we all benefit.

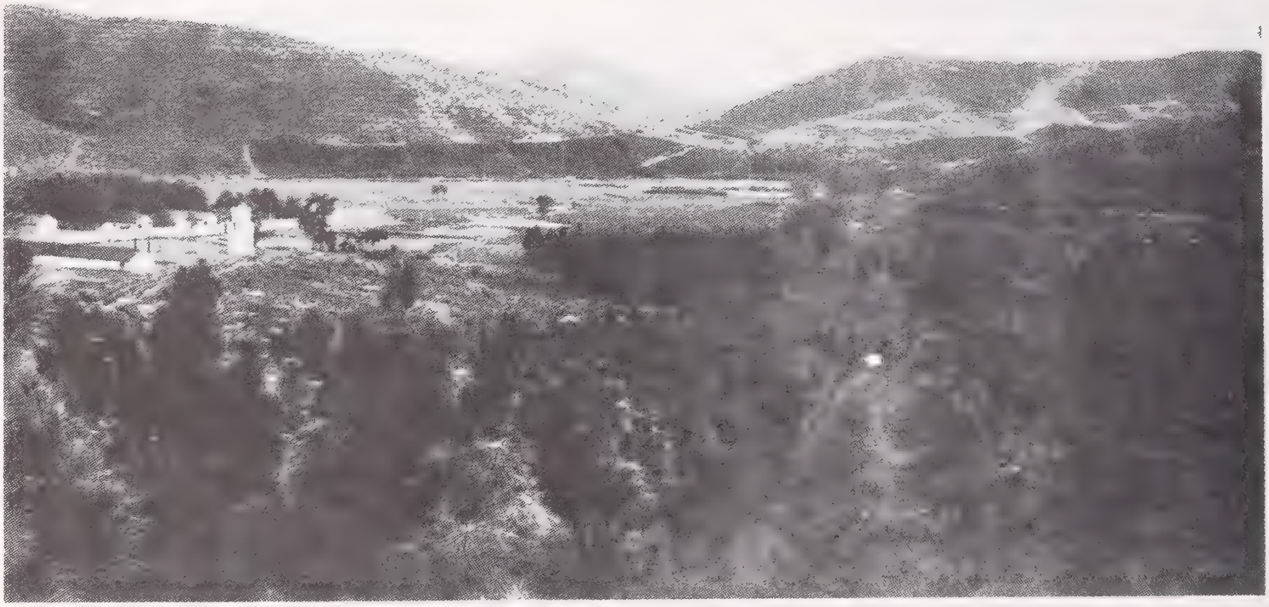

Figure 1. The Ever Happy Forest Farm in Zhejiang Province, The People's Republic of China. A slash pine plantation is in the foreground, with masson pine (Pinus massoniana Lamb.) on the ridgetops. In the valley rice is grown, and on the lower slopes there are tea plantations.

TREE BREEDING IN INTERNATIONAL FORESTRY

TEN YEARS OF INDUSTRIAL TREE IMPROVEMENT IN COLOMBIA

William E. Ladrach [1]

Abstract. Tree improvement is being carried out at three levels: 1) species, 2) provenance and 3) mother tree selection. Grafted seed orchards have been established for *Cupressus lusitanica* (5 ha., 1977) and *Pinus patula* (5 ha., 1981). Over 200 species have been tested and seed stands or improved seed stands exist for *P. kesiya*, *P. oocarpa*, *Gmelina arborea*, *Eucalyptus grandis* and *E. camaldulensis*. Important aspects of the program include cooperation in international provenance tests, local Colombian cooperation in progeny tests and an open-door policy with respect to research information, with reports distributed in both Spanish and English in many parts of the world.

INTRODUCTION

Cartón de Colombia, S.A., has been supplying paper packaging products for Colombian commerce since it's conception in 1944, when the first paper was produced exclusively from recycled wastepaper. In 1959, with increasing demand for packaging and with government support, the Company established the first kraft pulp mill in the world to use mixed tropical hardwoods to produce a uniform short fiber kraft pulp, and in 1970 began a reforestation program in the Andean region, planting tropical conifers on marginal agricultural lands as a means of replacing imported long fiber pulp with a nationally grown product. As a support for this forestry effort, a formal forest research program was established in 1973 with one of the objectives being tree improvement. Current planting goals are 2300 hectareas per year (1400 with coniferous species and 900 with broadleaf species), and the forest plantation utilization has now been expanded to include, not only pulp for paper packaging, but also bleached pulp for writing papers, as well as solid wood products, including treated posts and poles.

There are several limitations on tree improvement research and the development of a tree improvement program within the industrial situation just described. First, with a calculated plantation land area totalling approximately 30,000 hectareas, the forest research staff must be kept modest, which in our case is three professionals and two technicians. Although tree improvement in its broadest sense is the largest function of this research group, it is still only a part of the overall research program. Third, due to varied site conditions, many species are used for operational reforestation, several for the first time in Colombia on an operational basis, which in itself injects a rather large risk factor into investment decisions. Likewise, since industrial forest management as well as tree improvement are new fields in Colombia, and since Cartón de Colombia is the leader in both, we cannot turn to local government or university organizations for much technical assistance or information, but rather have to depend heavily on imported education, experience and technology.

---

[1] Director of Forest Research, Cartón de Colombia, S.A., Apartado Aéreo 219, Cali, Colombia.

Tree improvement strategies have been developed by which to deal with the variables and limitations mentioned (Ladrach, 1982), the main elements of which are 1) species selection and utilization, 2) provenance research and 3) land race mother tree selection. Tree improvement is carried out simultaneously at all three levels in the research program, depending upon the species, the accessibility of seed and the relative importance of the species being considered.

SPECIES SELECTION AND UTILIZATION

Plantations

Initial species selections were based on observations of limited plantation areas in other parts of Colombia and by comparison with other tropical countries with similar ecological conditions, especially in East Africa which has a long tradition of reforestation. In the conifer program, four species were used initially: *Cupressus lusitanica* Mill., and *Pinus patula* Schl. et Cham., both of which had been planted previously in Colombia, and *Pinus oocarpa* Schiede and *Pinus kesiya* Royle ex Gordon, which had not been used for commercial reforestation, the last being introduced by the Company in 1971.

Plantation observations also resulted in some initial provenance improvement and seed source improvement. For example, it was early recognized that *P. oocarpa* provenances from Central America performed better in Colombia than those from Mexico, and seed was purchased accordingly. Likewise seed purchases were concentrated with dealers who personally supervised their own collections from good phenotypes as opposed to intermediaries who purchased open market seed. Considerable improvement in form and growth of *P. patula* was obtained in this manner. We now know personally most of our international seed suppliers and have visited several areas of seed collection.

Species Trials

More than 200 tree species have been or are being tested for their potential use in reforestation. At this initial species selection level, major differences are being evaluated for a large number of species on many sites and the design used is an arboretum, in which each species is planted as a square plot, usually of 36 trees, without replication, on a uniform site. Ten such arboreta have been established, the largest with over 100 species.

Initially in the arboretum, the species is given maximum care including intensive site preparation, fertilization, regular weedings and sometimes initial irrigation to insure first year survival; once a promising species has been identified, then further testing under normal operational conditions is employed. In addition to the technical aspects, the arboreta are usually situated where they have demonstrative value as well. Field tours through the arboreta have become everyday programs with favorable public reactions; visitors have included students,employees, foresters, environmentalists, legislators, generals, cabinet ministers and presidents.

With limited resources, the simple design of the arboretum has permitted the testing of a large number of species and, in spite of the lack of statistical analyses, they have produced valuable information (Table 1). Arboretum growth data have served as a reliable first indication of plantation performance and, in the case of the arboretum in the Caribbean Coastal Plain, alternate and highly successful species were found for operational use where initial species selections for reforestation had failed.

Table 1. Species Developed For Reforestation in Colombia.

Species	Altitude meters a.s.l.	Stage
Cupressus lusitanica Mill.	1500-2300	Operational
Cupressus sempervirens L.	2000-3000	Operational
Pinus patula Schl. et Cham.	1500-3000	Operational
Pinus kesiya Royle ex Gordon	1300-2200	Operational
Pinus oocarpa Schiede	1500-2500	Operational
Pinus taeda L.	2000-3000	Pilot Project
Pinus caribaea Morelet	1000-1700	Pilot Project
Pinus chiapensis Andersen	1600-2000	Pilot Project
Pinus pseudostrobus Lindl.	1500-2500	Final Research
Pinus maximinoi H.E.Moore	1500-2500	Final Research
Eucalyptus grandis Hill ex Maid.	1500-2000	Operational
Eucalyptus globulus Labill.	2200-2700	Operational
Eucalyptus tereticornis Sm.	0-1400	Operational
Eucalyptus camaldulensis Dehn.	0-1400	Operational
Gmelina arborea Roxb.	0-1000	Operational
Cassia siamea Lam.	0-1000	Pilot Project
Bombacopsis quinnata(Jacq)Dugand	0- 500	Pilot Project
Tabebuia rosea D.C.	0- 500	Pilot Project

Seed Stand Development

Seed stands are being utilized for the local production of seed as a means of reducing dependence on imported seed and also as a means of capturing some land race adaptive traits. Unimproved seed stands have been developed for Pinus kesiya, P. oocarpa, Gmelina arborea, and Eucalyptus camaldulensis. These have been thinned from below and reduced, generally, to 100 trees per hectare; they are fertilized annually and maintained free of weeds.

Trees resulting from seed of the G. arborea and E. camaldulensis stands are equal to or better than those of the best non-selected provenances in comparative tests. No such differences have yet been observed for the pines, but it is hoped that the trees from the P. kesiya seed stands will show a lower incidence of fox-tail than those from imported seed.

PROVENANCE TRIALS

Species/Provenance Trials

Besides the arboretum species trials, additional studies have been established where several species are tested in replicated designs but with several provenances per species. In some tests a single species is predominant with many provenances represented while other species are included with only one or two provenances to serve as comparable checks. These tests are usually replicated on more than one site.

Most of these studies have been developed through cooperation in international trials sponsored by C.F.I., Oxford, England; C.S.I.R.O., Canberra, Australia; and DANIDA, Humlebaek, Denmark. Since these are considered as intermediate studies and, again, due to limited resources in personal, funds and homogeneous areas for installing them, only three replications per site are used in most cases (Table 2). Likewise, since early and fairly large differences between provenances are expected, and often found, individual plots are usually in rows of from 6 to 10 trees, and the studies are carried for short periods of time, usually to half rotation age which for Pinus and Cupressus is 8 years and for Gmelina and Eucalyptus, 3 years.

An advantage of this design is the potential for conversation of the trials into improved seed stands after the final evaluation. A selection is made leaving only the best species, the best provenances of that species and the best individual in each rowplot of the best provenances. Improved seed stands have already been developed by this procedure for Eucalyptus grandis Hill ex. Maiden and Eucalyptus camaldulensis Dehn. Additional stands will be developed this year for Gmelina arborea Roxb. and Eucalyptus globulus Labill. Initial commercial plantings with seed from these seed stands show visible advantages in growth over non-improved plantings from imported and locally produced seed.

Table 2. Species/Provenance Trials Installed By Cartón de Colombia.

Year	Principal Genus	Species/ Provenances	Sites	Reps./Site	Trees/Plot
1972	Pinus caribaea	2/6	1	2	200
1975	Gmelina	1/5	1	1	10
1975	Eucalyptus	6/16	2	4	10
1976	Pinus taeda	4/15	2	3	10
1977	Pinus a/	11/32	4	3	10
1977	Eucalyptus b/	5/32	6	3	10
1978	P. pseudostrobus	4/16	1	3	36
1978	Pinus a/	13/56	3	3	10
1979	E. grandis b/	4/44	2	3	8
1979	E. globulus b/	4/43	2	3	8
1979	E. saligna	4/25	1	3	8
1979	E. viminalis b/	2/11	1	3	8
1980	Gmelina c/	1/16	2	3	10
1980	Leucaena d/	2/13	3	3	10
1981	Eucalyptus e/	37/46	2	5	6
1981	Gmelina c/	1/14	2	3	36

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a/ C.F.I., Oxford, England, international provenance trials.

b/ Seed obtained from C.S.I.R.O., Canberra, Australia.

c/ DANIDA/FAO, Humlebaek, Denmark, international provenance tests.

d/ Seed obtained from C.I.A.T., Palmira, Colombia.

e/ Seed supplied by Tasmanian Commission of Forestry and C.S.I.R.O., Australia.

Provenance/Family Trials

Once a species and provenance are proven outstanding, trials are made of open-pollinated progeny of seed collected by mother tree in the original stands, or collected from select trees in seed orchards abroad. Cartón de Colombia staff have made individual tree collections by provenance in Central America, but for the most part such seed is obtained through international cooperation with CAMCORE and N.C. State University, Raleigh, North Carolina; C.F.I., Oxford, England; and through exchanges with other national organizations including the Forest Research Centre, Zimbabwe; the Kenya Forest Department; Mondi Timber Company, Republic of South Africa; and the Forestry Research Institute, Malawi.

Many of these studies are designed with nine replications, grouping families by provenance, with individual rowplots of six trees each and are established on only one site (Table 3).

Under Andean conditions, where uniform topography is scarce and flat topography scarcer still, such studies present difficulties in their establishment. For example, the C.F.I. second stage *Pinus oocarpa* study installed in Colombia in 1982 involves 100 families, separated into two sets with 9 replications each; at a spacing of 2.5 x 3 meters and with two border rows for isolation, this study covers 5 hectares.

Table 3. Provenance/Family Trials Installed by Cartón de Colombia.

Year	Species	Provenances	Families	Reps.	Trees/Plot
1976	Pinus taeda a/	—	24	3	10
1977	Cupressus lusitanica b/	6	23	3	10
1978	Pinus taeda a/	—	52	6	6
1981	Pinus oocarpa c/	7	33	9	6
1981	Eucalyptus grandis d/	7	80	4	6
1981	Pinus patula e/	6	22	3	10
1981	Pinus kesiya f/	3	12	6	6
1981	Cupressus lusitanica g/	6	15	3	6
1982	Pinus oocarpa h/	1	113	9	6
1982	Pinus tecunumanii Sch. c/	2	25	9	6
1982	Pinus oocarpa j/	9	100	9	6
1982	Pinus caribaea j/	9	89	9	6
1983	Pinus chiapensis c/	1	8	9	6
1983	Pinus oocarpa k/	7	36	9	6

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a/ N. C. State Pine Coop., good general combiners of loblolly pine, international trials.

b/ Seed supplied by E.A.A.F.R.O., Kenya, and Tropical Sci. Inst., Costa Rica.

c/ CAMCORE Cooperative study, Guatemala.

d/ Seed supplied by the Forest Research Centre, Zimbabwe, and Mondi Timber Co., South Africa.

e/ Seed supplied by the Forestry Research Institute of Malawi.

f/ Seed supplied by C.S.I.R.O., Australia, and SAPPI, South Africa.

g/ Seed supplied by the San Lucas Toliman Parish, Sololá, Guatemala.

h/ CAMCORE Cooperative Study, Belize.

j/ C.F.I. second stage international provenance trials.

k/ CAMCORE Cooperative study, Guatemala and Honduras.

With this design, such studies are convertible to seedling seed orchards at half rotation age, which action is planned. This then, will allow for a rapid expansion in the local production of genetically improved seed, which amply justifies the installation efforts in such studies.

LAND RACE MOTHER TREE SELECTION

Species And Characteristics For Selection

The species to be chosen for an individual tree selection program, above all else, have to be commercially planted at a sufficiently large scale in order to recover the investments in the selection process, seed orchards and progeny tests. This is, perhaps, an obvious fact to geneticists, but it has been overlooked by some institutional administrators who program research goals. Secondly, there must already be a sufficiently large plantation base in existence from which to make mother tree selections, and which will result in a significant selection differential (Jett, 1975).

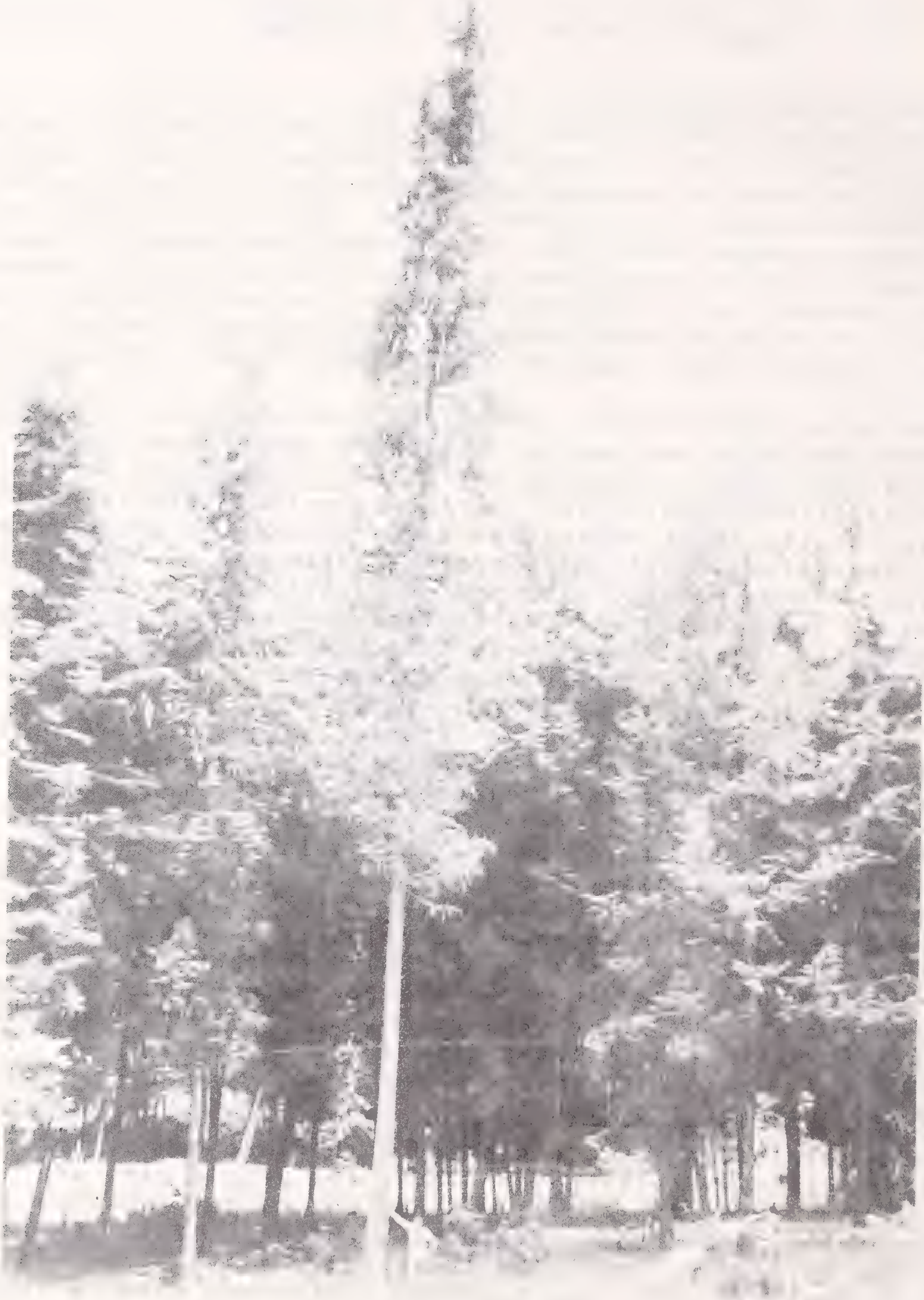
At the beginning of Cartón de Colombia's tree improvement program in 1973, there were only two species which met these requirements, these being Cupressus lusitanica Mill. and Pinus patula Schl. et Cham. An additional reason for initiating mother tree selections of cypress was the large observable difference in height between trees in plantations, indicating great genetic variability within the species. Pinus patula, although more uniform in tree size than cypress, demostrated wide variations in wood specific gravity between trees in initial samplings, thus indicating a sizeable potential gain in this trait through selection.

The tree selection system utilized is based upon that developed in the North Carolina State Tree Improvement Cooperative (Zobel, 1974). Five tree characteristics were selected for improvement: 1) resistance to insects and disease, 2) volume, 3) straightness, 4) wood quality and 5) crown form. Two grading concepts are utilized, these being relative and absolute. For example, crown form is graded relative to the best five neighboring trees whereas straightness is graded as an absolute value irrespective of the other trees. The wood quality is graded by both criteria, and must be equal to or better than the average established for that species and age but must also be superior to the average of the best five neighboring check trees (Figure 1).

Grafted Seed Orchards and Progeny Tests

Scions from selected trees are grafted into clone banks, holding 5 ramets per clone. Grafting techniques for patula pine are similar to those used for loblolly pine, but cypress, having a much finer scion, presented difficulties and only 12 to 15% take was obtained initially. With the technical visit of Dr.Frederick Owino to Colombia in 1975, the grafting techniques used in Kenya were adopted and the average success for all the cypress seed

Figure 1. A select *Cupressus lusitanica* 15 years old in the Seminary of Medellín, Colombia, is 6.6 meters taller than the average of the best five neighboring check trees.



orchard grafting in 1977 was increased to 92% (Figure 2).

The cypress seed orchard was planted according to a computer design created by N. C. State University for 30 clones. Five hectares of orchard were established, based on yield estimates from Kenya (Owino, 1975), utilizing an initial spacing of 5 by 10 meters. Final thinning should leave the orchard with a minimum of 15 clones and about 100 trees per hectare. Cypress is a heavy and early seed producer and the fifth year crop yielded 215 kilograms of seed from 22 clones. Forced air separation of good seed has resulted in a cleaned yield of 120 Kg. with an average germination of 23% which is still below the 40% germination which has been obtained from cleaned seed in older plantations.

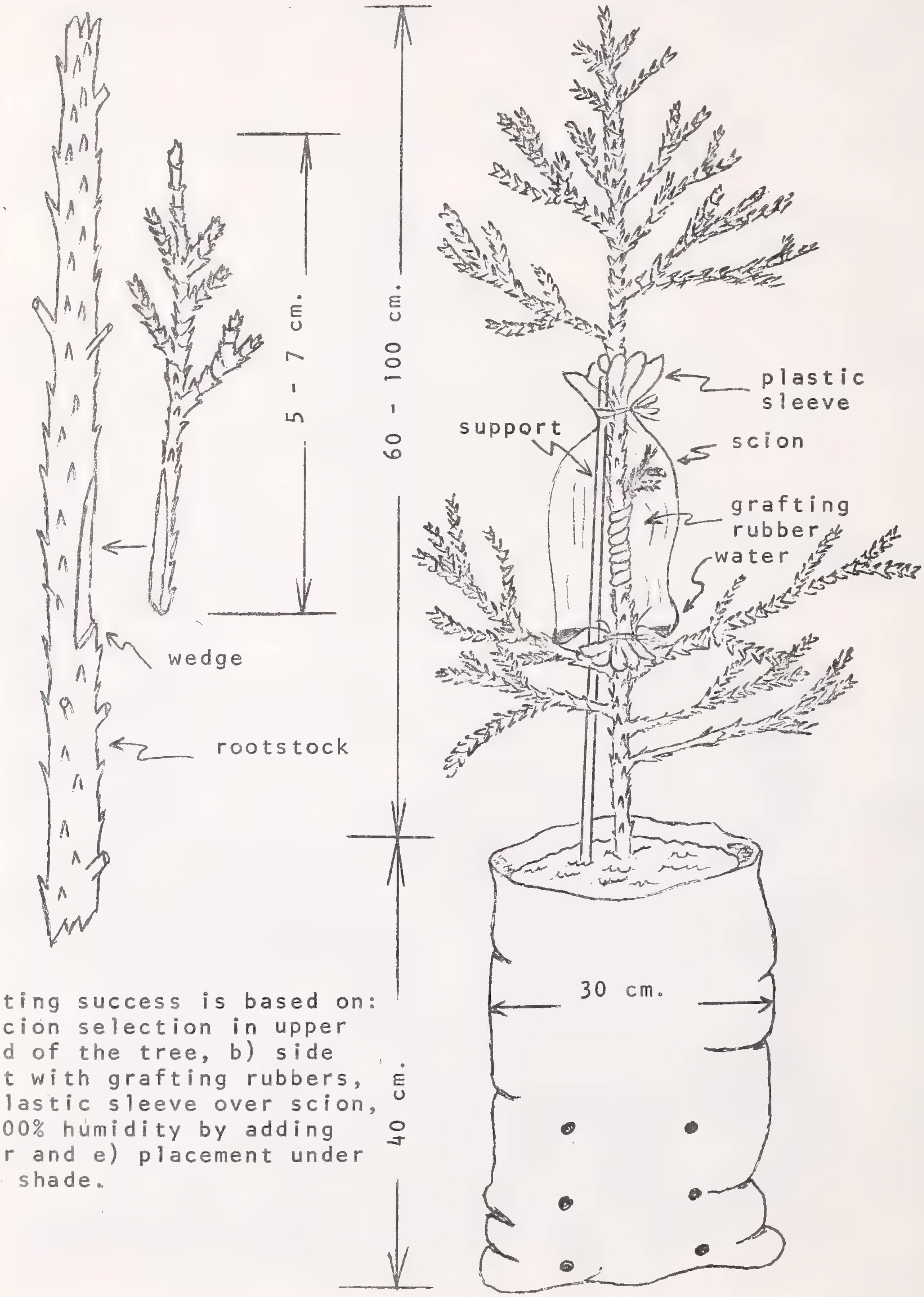
The patula pine orchard was initiated in 1981, again using the 30 clone N. C. State design. Five hectares are initially being installed, but additional area will be needed to produce all the seed required for reforestation. Mr. Neville Denison of Mondi Timber Company, South Africa, recommended during a visit in 1977 that we locate the patula pine seed orchards above 2000 meters altitude in order to obtain optimum seed production. Due to the lack of level terrain at these heights, the first orchard was located at 1850 meters, but all attempts will be made to comply with his recommendation for the expansion orchard. Incompatibility has not been a problem thus far for either cypress or patula pine; only one cypress clone was rejected after it could not be held successfully even when grafted on rootstock from seed of the same mother tree.

Not all trees selected had seed and, therefore, open-pollinated progeny tests have not been established to date for all select trees. Cypress o. p. progeny tests have thus far been established for 28 trees and tests have been established at 6 locations in Colombia, through cooperation by the Colombian forest service (INDERENA), the public utilities companies of Bogotá (C.A.R.) and Pereira (EE.PP. de Pereira), the secretary of agriculture in Antioquia (Medellín) and the Archdiocese of Medellín. Besides permitting the establishment of the tests on their lands, some organizations have actively participated in the site preparation, planting, care and measurement of the studies; especially important have been the efforts of INDERENA in Medellín and the C.A.R. in Bogotá, this being accomplished with no formal written agreements.

The oldest progeny tests will complete 8 years during 1983, at which time final evaluations will be made, this being considered half rotation age. Earlier evaluations at three years of age indicated gains of 50% in volume, 13% in height, 2% in straightness and no gain in crown form compared to commercial check lots (Ladrach & Gutierrez, 1980). These gains concur with those for cypress in Kenya after 10 years (Dyson & Raunio, 1977).

Controlled crosses have been tried with cypress on a pilot basis

Figure 2. Grafting Technique For Cupressus lusitanica.



Grafting success is based on: a) scion selection in upper third of the tree, b) side graft with grafting rubbers, c) plastic sleeve over scion, d) 100% humidity by adding water and e) placement under half shade.

and have been successful, but controlled crosses have not been carried out by clone for progeny tests to date. Poor pollen production is a problem with cypress, but this has been increased to acceptable levels for pollen collection by spraying gibberillic acid GA3 on the foliage once per month for six months at concentrations of 100 p.p.m. in ethyl alcohol (Gutierrez, 1980).

Tree Breeding Strategies

Continued tree selection must depend upon the introduction of additional material from outside Colombia and the provenance/family tests already described will be the primary source of this material. Even so, with the limited genetic base available, no more than two generations of mother tree selection are anticipated in the present program (Figure 3).

Nonetheless, early indications are that the genetic gains from this modest program with tropical species will be substantial and beneficial, due to the observable natural variation within the species and between provenances as well as to the response of these introduced species to Colombian conditions. Likewise, due to the rather large risk factor of working with introduced species, such a program is of key importance in assuring the future success of the overall reforestation effort.

OTHER IMPORTANT CONSIDERATIONS

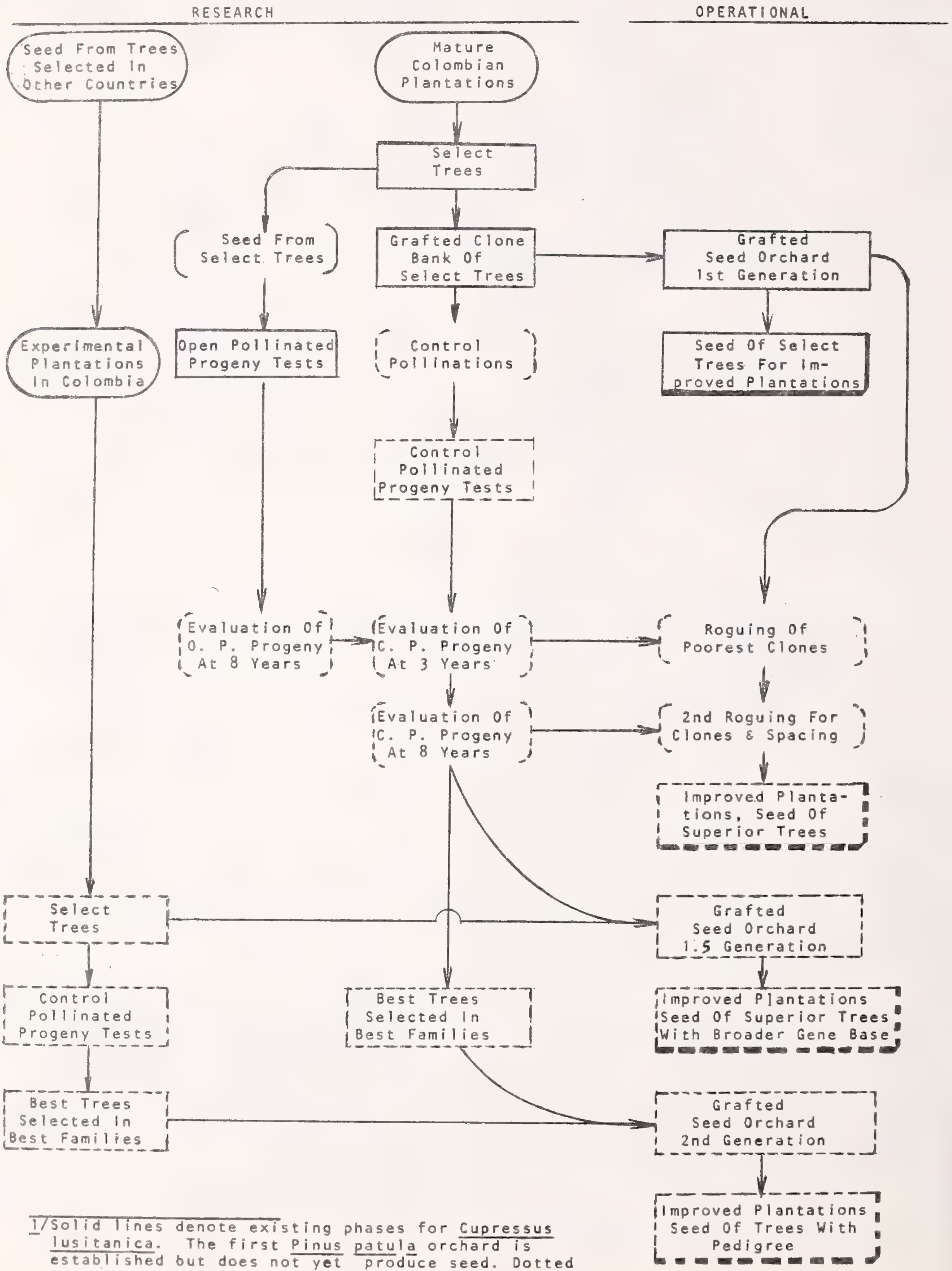
For a tree improvement program within one company to be successful, there must be constant contact with outside institutions working in this field on an international level. One of the best methods to achieve this contact is by participating in international provenance and progeny tests, where it is possible to obtain research lots of seed from many provenances, otherwise unattainable, and to compare results locally with the results of similar tests in other parts of the tropical world.

Equally important is to invite foreign experts to see and advise on the program in the field, and conversely, local personnel have to maintain themselves current of research in other parts of the world through publications and travel. Without this constant contact with the outside world, a small local program would be seriously handicapped in its scope and results.

Although there is no official tree improvement cooperative in Colombia, the cooperative efforts of local agencies have been instrumental in the gains achieved to date. Many of the initial tree selections are the result of preselections by personnel in governmental agencies and public utilities working on their own lands. Site preparation, planting and periodic measurements are in large part the result of close cooperation as well.

This type of open collaboration is, of course, a two-way proposition,

Figure 3. Tree Breeding Strategy For Land Race Conifers.


RESEARCH
OPERATIONAL
Seed From Trees Selected In Other Countries
Mature Colombian Plantations
Select Trees
Seed From Select Trees
Grafted Clone Bank Of Select Trees
Grafted Seed Orchard 1st Generation
Experimental Plantations In Colombia
Open Pollinated Progeny Tests
Control Pollinations
Seed Of Select Trees For Improved Plantations
Control Pollinated Progeny Tests
Evaluation Of O. P. Progeny At 8 Years
Evaluation Of C. P. Progeny At 3 Years
Roguing Of Poorest Clones
Evaluation Of C. P. Progeny At 8 Years
2nd Roguing For Clones & Spacing
Improved Plantations, Seed Of Superior Trees
Select Trees
Grafted Seed Orchard 1.5 Generation
Control Pollinated Progeny Tests
Best Trees Selected In Best Families
Improved Plantations Seed Of Superior Trees With Broader Gene Base
Best Trees Selected In Best Families
Grafted Seed Orchard 2nd Generation
Improved Plantations Seed Of Trees With Pedigree

[1] Solid lines denote existing phases for *Cupressus lusitanica*. The first *Pinus patula* orchard is established but does not yet produce seed. Dotted lines denote planned phases.

and the reports of field research are distributed freely in return. All research reports on all phases of forest research are sent out in both Spanish and English to agencies interested in tropical forestry in many parts of the world simultaneously with the distribution of these same reports to personnel within Cartón de Colombia. Because of this open-door policy with regard to forest research information, the professional image of the Forestry Division has improved substantially in the past ten years as well as resulting in cooperation, seed received for international trials and many reports received in return for those sent. Besides technical report distribution, field tours and documents dealing with a particular phase of forest research are presented to about 250 Colombian professionals each year.

CONCLUSIONS

An industrial tree improvement program not only can be, but must be carried out when working with introduced species to assure the selection of species and provenances which result in the maximum gain at minimum risk. Without such research the gain is less and the risk increases. Although the tendency is to initiate land race mother tree selections in a new program, and this is commendable, emphasis also has to be placed on species trials and provenance trials, especially for untested or little tested genetic material.

Study designs for testing of expected large differences, such as between species, can be simpler than designs to find finer differences, such as between families of the same provenance. A design for provenance tests and family tests which allows for these studies to be converted to seed production has a distinct advantage over other designs where operational seed needs must be met; but other, long-term studies must also be installed in order to obtain growth and yield information. Again, research risk versus research gain have to be balanced in order to maximize the return on the research investment.

The long term success of an industrial tree improvement program such as that of Cartón de Colombia depends heavily on close contact and constant communication with institutions knowledgeable in the material. Without this contact, considerable time and effort can be wasted or utilized inefficiently and the risk of research error increases substantially. The dissemination of research information is of vital importance in creating and maintaining this communication, and the publishing of research information should be actively promoted at the administrative level to insure that long range research results are compatible with those of other international agencies and thereby will be beneficial to that particular company or industry in the long run.

LITERATURE CITED

Dyson, W.G. and A.L. Raunio. 1977. Revised heritability estimates for Cupressus lusitanica in East Africa. Silvae Genetica 26 (5-6): 193-196.

Gutiérrez, M., 1980. Aumentando la floración del cipres con giberelina. Mejoramiento de Bosques, Quinta Reunión Anual de Investigación Forestal, Cartón de Colombia. 157-159.

Jett, Jr., J.B. 1975. Objectives of a tree improvement program. Reunión anual de investigación forestal, Cartón de Colombia. p. 20-21.

Ladrach, W.E. y M. Gutiérrez. 1980. Logros genéticos con Cupressus lusitanica a través de seis años de mejoramiento de árboles en Colombia. Mejoramiento de Bosques, Quinta Reunión Anual de Investigación Forestal, Cartón de Colombia. 95-135.

Ladrach, W.E. 1982. Three different breeding strategies for forest species in Colombia, based on population size and available provenance research information. Proc., I.U.F.R.O. joint meeting of working parties on genetics about breeding strategies including multiclonal varieties. Lower Saxony Forest Res. Inst., Germany. Summary p. 222.

Owino, F. 1975. Que se ha aprendido a través de 60 años de experimentación con C. lusitanica en Africa Oriental. Informe de investigación forestal No. 11. Cartón de Colombia. 8 p.

Zobel, Bruce. 1974. Increasing productivity of forest lands through better trees. The S. J. Hall Lectureship in Industrial Forestry, University of California, Berkeley. 20 p.

STRATEGY FOR THE DEVELOPMENT OF CONSERVATION BANKS AND BREEDING PROGRAMS FOR CONIFEROUS SPECIES FROM CENTRAL AMERICA AND MEXICO

William S. Dvorak[1]

Abstract.--The urgent need to save populations of coniferous species in Central America and Mexico led several private forest industries in North and South America to form the Central America and Mexico Coniferous Resources Cooperative (CAMCORE) at North Carolina State University in 1980. In 1982, CAMCORE collected seed from over 800 selected trees in Guatemala and Honduras of 5 species: *Pinus tecunumanii*, *P. oocarpa*, *P. ayacahuite*, *P. pseudostrobus*, and *P. caribaea*. In 1983, collections will include 7 species of conifers, some of which are extremely endangered and have never been tested on a wide scale (e.g. *Abies guatemalensis*). Seed from these collections are planted on Cooperative members' land in conservation banks and provenance/progeny tests. The conservation banks are designed and managed as specialized breeding populations based primarily on site adaptability traits. Long-term breeding strategies are being developed to fully utilize this valuable genetic material for future generations. The provenance/progeny tests serve to locate the best provenances and families for further testing and development of adapted land races. Provenance x environment and genotype x environment interactions will be monitored in the provenance/progeny tests, which in the future, will be established on as many as 24 sites throughout Mexico, Central and South America, and Africa.

Additional Keywords: Conservation banks, multiple breeding populations, provenance/progeny tests, endangered species

INTRODUCTION

More coniferous species and varieties can be found in Mexico and Central America than in any other region of similar size in the world. Over 70 species, varieties, and forms of pines alone have been identified in this region (Jasso, *et al.*, 1978). New coniferous species are still being identified in Mexico and Central America, and as more of the pieces of this evolutionary puzzle fall into place, species and varieties originally assigned to one taxonomic complex will be reclassified and placed in more appropriate taxonomic

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groupings. The complex evolutionary puzzle is far from complete because species are still in the process of developing through intensive natural selection under a wide range of environmental conditions. The continuing process of speciation makes coniferous regions in Mexico and Central America some of the most genetically diverse in the world.

This tremendous genetic diversity of forest populations in Mexico and Central America gives foresters the opportunity to select and test a number of promising species and provenances to find those which are best suited for commercial plantations and reforestation programs in tropical and subtropical regions throughout the world. Many forestry organizations with low-elevation land in tropical regions currently plant thousands of hectares annually of Pinus caribaea var. hondurensis and Pinus oocarpa, species native to Mexico and Central America. Species from mid-elevation regions (1500-2000m) in Mexico and Central America such as Pinus patula and Cupressus lusitanica have also proven successful, as exotics, in parts of South America and Africa. Other species and varieties will undoubtedly prove valuable in exotic plantations and local forestry programs in the future.

Unfortunately, with each passing year, the chances diminish to test and utilize promising forest populations of endangered coniferous species from this region. The loss of these valuable genetic resources result from an onslaught of fuelwood cutters, shifting agriculture practices, sawmill activities, uncontrolled fires, over grazing, and disease and insect attacks (Gallegos, et al., 1980). A decade ago, 70% of all families living in Guatemala used wood as their main source of fuel (Venator and Muñoz, 1974). As a result of the increased population pressure and the high cost of petroleum, the demand for wood is even more intense today. It has been estimated that the pine forests in Guatemala are being reduced at the rate of 2.5%/year (Plant Resources Institute, 1981).

Are entire species and provenances in danger of being lost? In some cases, yes, especially in the fertile highland regions of Mexico, Guatemala, Honduras, and El Salvador. The need for more land on which to produce crops to sustain increasing populations requires conversion of forests to farm lands (Veblen, 1978). For example, Pinus tecunumanii stands are being methodically clear cut by farmers to make way for the planting of annual crops in the mountains of Guatemala and Honduras. Only small stands of several hundred trees still remain in some areas. Provenances of Pinus ayacahuite and Pinus pseudostrobus are also in danger of being lost in the highland areas.

Complete loss of a species or provenance is usually not the problem. The most common occurrence in Mexico and Central America is the reduction of forest populations into groups of remnant, highly degraded stands that retain little value as a source of genetic material for productive forestry programs. The disastrous reduction of these gene pools jeopardizes the chances for finding well adapted species and provenances for the marginal areas now being used for reforestation and plantations in the tropics and subtropics.

In 1980, several progressive forest industries from North and South America: Aracruz Florestal (Brazil), Cartón de Colombia, International Paper Company (U.S.A.), and the Weyerhaeuser Company (U.S.A.) began an immediate action program to preserve genetic material of coniferous species in Central America and

Mexico. These organizations formed the Central America and Mexico Coniferous Resources Cooperative (CAMCORE) at the School of Forest Resources, North Carolina State University. Between the time of its formation in mid-1980 to 1983, the Cooperative has grown to include ten active members from both the private and government forestry sectors in Brazil, Colombia, Venezuela, South Africa, and the United States, three honorary members from Central America and Mexico, and one contributing member (see Table 1). Initial conservation work began in Guatemala (1980) and expanded to include Honduras (1982) and Mexico (1983).

Table 1--Members of the CAMCORE Cooperative

Active Members

Aracruz Florestal (Brazil)
Cartón de Colombia
Cartón de Venezuela
CONARE (Venezuela)
COPINUS (Brazil)
EMBRAPA/IBDF (Brazil)
Jari Florestal (Brazil)
PIZANO/Monterrey Forestal (Colombia)
South African Forestry Research Institute
Weyerhaeuser Company (U.S.A.)

Honorary Members

BANSEFOR/INAFOR (Guatemala)
ESNACIFOR/COHDEFOR (Honduras)
INIF (Mexico)

Contributing Member

Crown Zellerbach (U.S.A.)

OPERATION OF THE COOPERATIVE

The CAMCORE program is divided into two phases, both of which occur simultaneously. Phase I deals with the collection of seed from species and/or provenances in Mexico and Central America that are being degraded, some of which are endangered. Phase II deals with using the seed collected from these endangered populations to establish conservation banks and provenance/progeny tests on the land of Cooperative members in Mexico, Central and South America, and Africa. The purpose of the conservation banks is to both maintain existing gene complexes and to produce new genetic combinations for use in breeding programs. The provenance/progeny tests serve to locate the best provenances and families for further testing and development of adapted land races (Dvorak, 1982). The underlying assumptions made in the CAMCORE program are:

1) The conservation effort is long-term, which, by necessity, requires dynamic advanced generation planning.

2) Gene conservation and breeding efforts can best be made compatible by designing and managing conservation banks as specialized breeding populations based on site adaptability and/or speciality traits (Namkoong, *et al.*, 1980).

Population Sampling

Seed collection activities in Central America and Mexico need to be concentrated in the populations where the probability of obtaining the greatest array of alleles is the highest. The greater the diversity of alleles conserved the better the chances for developing widely adaptive breeding populations in the future. Unfortunately, no "genetic maps" exist which show where the magnitude of genetic variation is the greatest. When CAMCORE collections are made in mountainous areas, sampling is in the direction of the greatest elevation gradient. For example, in a recent seed collection of *P. tecunumanii* on the mountain of Celaque in Honduras, sampling occurred through the elevation range of the species from 1520 to 2030 meters. Whenever possible, outlying populations are also included in the sampling.

CAMCORE selects between 35 to 50 of the phenotypically best dominant and codominant trees in a stand. It is the phenotypically best trees, not random ones, that are used in the program because both the conservation and testing of genetic material are the objectives. This system is possible because characteristics of adaptability are nearly always genetically independent of those of economic value (e.g. tree straightness) (Zobel and Talbert, 1983).

The highest priority in selection is given to stem straightness and branch habit because these are both reasonably highly heritable traits, and sizeable genetic gains can be made in the first generation through simple mass selection. Stem volume is given a lower priority in the selection system, although it is of importance. Seed, which are kept separate by mother tree, are collected from as many provenances of a species as possible. The seed are then distributed to CAMCORE members to establish conservation banks and the provenance/progeny tests.

Strategy for the Development of Conservation Banks

Cooperative members' forestry programs differ in many respects. Some CAMCORE organizations are just beginning species and provenance tests, while other agencies are well into advanced generation breeding programs. Some organizations have low-elevation lands and are planting *P. caribaea* and *P. oocarpa*, while others have high-elevation lands and are primarily interested in such species as *P. patula*, *P. pseudostrobus*, and *P. tecunumanii*. Some members are producing kraft-quality paper and cardboard boxes to meet local internal demands while other organizations are producing fine-quality paper for the competitive European market.

With the varied interests of CAMCORE members in mind, it was felt gene conservation and breeding efforts could best be made compatible by designing and managing conservation banks for each species in sets of multiple-breeding populations based primarily on site adaptability characteristics. Therefore, CAMCORE's first conservation banks of *P. caribaea* are being divided into wet-site and dry-site populations. Dry-site collections of *P. oocarpa* from Honduras and Guatemala have been grouped together in one bank but kept physically separate from the genetically different *P. oocarpa* from Mt. Pine Ridge, Belize. Species with a large elevational range such as *Pinus maximinoi* will be divided into high- and low-elevation populations. Other populations may be developed for adaptability to high pH soils, wind firmness, etc. Development of banks for speciality traits such as disease resistance will be done on an organization-by-organization basis depending upon individual needs. For those species which have never been adequately tested before such as Abies guatemalensis, only one conservation banks (population) will be initially established by each member.

The multiple population system is particularly advantageous because intensive development may be pursued in those sub-populations which justify more attention (Namkoong, et al., 1980). In the banks which prove to be of most value, controlled crosses will be made and the best performers incorporated into the next generation. For banks which contain a species and/or sub-population of secondary importance, management will be less intensive and include only open-pollinated seed collections to establish adaptive land races. Another option is to make crosses among banks to generate new and possibly more useful genetic combinations.

The advantage of having the banks on many sties in a number of different countries is that destruction of one by natural or man-made causes does not jeopardize the loss of the genetic material. In addition, by planting the banks in different countries under varying environmental conditions, selection pressures will vary and favor different genetic combinations (Palmberg, 1981).

The CAMCORE conservation banks consist of completely randomized single-tree plots and are established in areas where cone and seed production are thought to be good. The size of the banks range from 1 to 4 hectares for each sub-population and contain between 50 and 300 families. For instance, the P. oocarpa collections of 1980, 1981, and 1982 sampled dry-site regions from 15 provenances in Guatemala and Honduras. Cooperative members which have been with the program since its beginning have a genetic base of approximately 300 families in their P. oocarpa dry-site conservation bank. Genetic bases are kept as large as possible. Some organizations will have as many as 3 to 4 separate sub-populations (700 families) for the more important species. CAMCORE members are also encouraged to incorporate extra seedling material from the Commonwealth Forestry Institute's (C.F.I.) second-stage provenance/progeny tests into the banks. Seed exchanges have already occurred with C.F.I., and more are planned. Seed exchanges are also planned with the Queensland Forestry Department, the Danish International Development Agency (DANIDA), the South African Forestry Research Institute, the National Program of Forest Research (PNPF) Brazil, and the Forestry Research Center, Zimbabwe.

Provenance/Progeny Tests

The provenance/progeny tests are planted in a randomized complete block design, replicated nine times with six-tree family-row plots. Enough seed is distributed to CAMCORE members to test provenances and families on a number of sites in several countries so that provenance x environment and genotype x environment estimations can be determined. The provenance/progeny tests are planted where plantation and reforestation activities are a prime concern, and therefore, may or may not be in the same vicinity as the conservation banks. For example, the provenance/progeny tests and conservation banks of Aracruz Florestal (Brazil) are planted in the same region because the area is excellent for seed production and also happens to be the type of land on which plantations will be established. PIZANO/Monterrey Forestal (Colombia) has placed the majority of its provenance/progeny tests near the coast where its main planting activities are, and its conservation bank in the interior of the country, several hundred miles away. This is because the site in the interior of the country has higher and more consistent rainfall which offers more security for the long-term survival of the banks.

Approximately 60% of the families included in the conservation banks are also established in the provenance/progeny tests for any one organization. Those families not tested by one organization are tested by other members at different sites. Therefore, exchange of genetic material among members will play an important role in the development of breeding programs in the future as it has for the North Carolina State-Industry Tree Improvement Program. All data from the provenance/progeny tests are analyzed at North Carolina State University. Table 2 summarizes the similarities and differences between the CAMCORE provenance/progeny tests and conservation banks.

Table 2--Similarities and differences between provenance/progeny tests and conservation banks for each organization

	Provenance/Progeny Test	Conservation Bank
Purpose:	Find superior provenances and families	Hold and further develop genetic material for future use
Design:	Randomized complete block	Completely randomized single-tree plots
No. of provenances included:	All that were collected	All that were collected
No. of families included:	Approximately half of those collected	All that were collected for which there were enough seedlings
Spacing:	3m x 3m	3m x 3m
Location:	On sites to be used for wide scale reforestation or commercial plantations	On sites where cone and seed production are thought to be good

RESULTS

Since the beginning of the program in 1980, seed have been collected from approximately 1,000 selected mother trees of 5 coniferous species: Pinus ayacahuite, P. caribaea, P. oocarpa, P. pseudostrobus, and P. tecunumanii. In 1983, this list of species will also include P. chiapensis and A. guatemalensis. Exploration in Central America has led to the discovery of new areas of P. tecunumanii. In 1981, CAMCORE's first conservation banks and provenance/

progeny tests of P. tecunumanii and P. oocarpa were established in Brazil, Colombia, and Venezuela. In 1983, government forestry organizations in Guatemala, Honduras, and Mexico began establishing conservation banks of P. oocarpa. At present, approximately 25 hectares of conservation banks and 50 hectares of provenance/progeny tests have been established by CAMCORE members. Results from the provenance/progeny tests will be made available when studies become older.

SUMMARY

The Cooperative program has grown, even during a period of economic recession, because a group of progressive forestry organizations are aware that action must be taken now in order to preserve the valuable coniferous resources in Central America and Mexico. During the next several years, CAMCORE activities will be directed toward seed collections of endangered mid- and high-elevation coniferous species. Future success of the program rests on the continued cooperation from the honorary members in Guatemala, Honduras, and Mexico, the strong support from active members in North and South America, and South Africa, the development of dynamic strategy which coordinates gene conservation efforts and tree breeding concerns, and the exchange of seed with other international organizations to maintain broad genetic bases.

LITERATURE CITED

Dvorak, W. S. 1982. Estrategia para las Operaciones de la Cooperativa de Recursos de Coniferas de Centro America y Mexico (Strategy for the Operations of the Central America and Mexico Coniferous Resources Cooperative), Venezuela Forestal, No. 5, August, 1982, pp. 2-8.

Gallegos, C. M., B. J. Zobel, and W. S. Dvorak. 1980. "The Combined Industry-University-Government Efforts to form the Central America and Mexico Coniferous Resources Cooperative." IN: Proceedings of an International Symposium, IUFRO, Institute of Tropical Forestry, Rio Piedras, Puerto Rico, pp. 361-366.

Jaso, M. Jesús, Raúl Villarreal C., Fernando Patiño, and Teobaldo Eguiluz P. 1978. Recursos Geneticos Forestales de México. IN: Analisis de los Recursos Geneticos Disponibles a México, Sociedad Mexicana de Fitogenetica, A. C., pp. 423-439.

Namkoong, G., R. D. Barnes, and J. Burley. 1980. A Philosophy of Breeding Strategy for Tropical Forest Trees, Commonwealth Forestry Institute, Department of Forestry, University of Oxford, England, 67 pp.

Palmberg, Christel. 1981. A vital fuelwood gene pool is in danger. IN: Unasylva 33(133):22-30.

Plant Resources Institute. 1981. Present Utilization and Potential Regeneration of Pinaceae in the Highlands of Tropical Mexico and Guatemala, Final report presented to U. S. Man and Biosphere Program. U. S. Department of State, Washington, D. C.

Veblen, T. T. 1978. Guatemalan Conifers, Unasylva 29(118):25-30.

Venator, C. R. and J. E. Muñoz. 1974. Containerized tree production in the tropics. IN: Proceedings of the North American Containerized Forest Tree Symposium, Great Plains Agricultural Council, Publ. No. 68.

Zobel, B. J. and J. Talbert. 1983. Applied Tree Improvement. John Wiley & Sons. (in press)

PINUS CARIBAEA CONE MATURATION IN PUERTO RICO

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Abstract.--Plantations of Pinus caribaea var. hondurensis located on a variety of sites in Puerto Rico provide an opportunity to study the effects of topography, soils, climate and tree age on cone production.

Factors which appear to favor the production of viable seeds are well-drained soil, a seasonal rainfall pattern and wide spacing in plantations. Adequate pollen production and dispersion are rarely found in the moist and wet forest zones where annual rainfall exceeds 80 inches (2032 mm).

Additional keywords: Tropical pines, seed production, pollen dispersion.

INTRODUCTION

Puerto Rico is a U. S. Commonwealth and a part of the Southern Region of the USDA Forest Service. The Forest Service involvement in Puerto Rico includes:

--The Caribbean National Forest: 28,000 acres of land including the only tropical rain forest in National Forest ownership.

--The Institute of Tropical Forestry: a branch of the Southern Forest Experiment Station.

--State and Private Forestry: the technical assistance and training branch of the Forest Service.

The work reported here was done as a part of the tree improvement training and technical assistance provided to the Puerto Rico Department of Natural Resources - Forest Service.

Puerto Rico shares a history of land exploitation similar to the United States. By 1935 85% of the natural forest had been cut-over. The continual pattern of small ownerships, cut and burn agriculture and unstable economy have combined to create a tremendous need for reforestation. Also the uncertain future of both sugar cane and coffee has provided an increasing demand for reforestation on many sites.

SITES - SPECIES

Due to the tremendous variation in elevation (sea level to over 1,000 meters), rainfall (36-180 inches:900-4600 mm) and soils (volcanic, granitic, limestone and serpentine) a great variety of sites exist on the island. Since the native species have been severely depleted a good opportunity exists for exotics. Notable among these are mahogany (Swietenia macrophylla, S. mahogoni, and the putative hybrid S. macrophylla x mahogoni), teak (Tectona grandis) mahoe (Hibiscus elatus), Eucalyptus alba, grandis, robusta, and deglupta, Pinus oocarpa and Pinus caribaea.

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PINUS CARIBAEA

Plantations of tropical pines were established in the early 1960's in Puerto Rico with provenance tests, spacing studies and some unreplicated species trials. Honduras pine (Pinus caribaea var hondurensis) has been the best overall performer when all pine sites are considered. The Belize Mountain Pine Ridge source has consistently outgrown other sources of Honduras pine in Puerto Rico as it has in many other tropical areas.

Honduras pine:
- a. survives and grows well on a variety of soils within the rainfall zones of 50 to 120 inches (1270 to 3048 mm).
- b. produces wood of acceptable quality for posts, poles and lumber.
- c. can be regenerated at reasonable cost with seedlings grown in plastic bags or styroblocks in shade houses.

SEED QUALITY

Early efforts at Honduras pine cone collection and seed processing were discouraging with yields of 10, 15 or 20 seeds per cone. Venator (1973) found 68% empty seeds in local collections in Puerto Rico. Recent cone collections on the island (1982) have resulted in an average of less than 10 seeds per cone with only 50% filled seeds. Many of the cones contained primarily first year aborted ovules (Bramlett et al 1977).

FLOWERING OF PINUS CARIBAEA

Puerto Rico is located at 18° N latitude. This is well within the latitudinal band of 9-27° N which Gallegos (1980) identified as the optimum environment of Honduras pine for seed production. In Puerto Rico however multiple sets of female flowers are often produced in the high rainfall areas (>80"-2032 mm) but male flowers are erratic in appearance. Ibrahim (1977) commented on a similar situation in Malaysia (3° N) where pollen production often occurred too late to be effective. In addition, the lack of air movement in the humid tropical environment limited pollen dispersal. Attempts at controlled pollination failed, perhaps due to excessive temperature (32° C). Ibrahim extracted only 3-6 viable seeds per cone.

The association of flowering with type of climate was recently mentioned by Delwaulle (1982) referring to the flowering of Honduras pine in the Congo (5° S). In the southern Congo Honduras pine produces good seed crops from plantations and seed orchards even though it is in a "non-productive" latitudinal zone. Delwaulle's explanation for this is the marked dry season (4-5 months) during which flowering and seed production occur. Mean annual precipitation is 47" (1194 mm) which with the dry season places this area in a Köppen climatic type Aw (Tropical Savannah climate). The natural range of Honduras pine in Belize falls in this climatic type as does other areas of good seed production such as northern Nigeria and Uganada.

The Anasco area of Western Puerto Rico averages 2090 mm (82") of rainfall but a dry period occurs from December to March during which time flowering occurs.

In this area flowering and seed production appear to follow a more "normal" development as attested by abundant natural regeneration on the edges of 10 to 18 year-old plantations. It would appear therefore that this area fits Delwaulle's hypothesis.

The higher rainfall areas of eastern Puerto Rico referred to earlier fall into a Köppen type Af (rain forest, wet tropical lowlands) where conditions are continuously wet and there is no definite dry period. Other areas in this climatic type are French Guiana, the Phillippines and parts of Brazil (Delwaulle 1982).

Fiji (17° S) would appear to be an exception to Delwaulle's hypothesis since flowering and seed production of Honduras pine has been outstanding in an area of high annual precipitation. However, the climate does include a dry season, corresponding to a Köppen type Am (Monsoon climate). Cone maturation progresses from high elevation (450 m) in mid-December to low elevation (30-100 m) in mid March (Dvorak 1977). Cones from the high elevation plantation have the highest percent of good seed (95%) and also the highest germination percentages (57-72%).

CONE MATURATION STUDIES

Young plantations on a variety of sites in Puerto Rico have been selected for conversion to seed production areas. In the process of establishing these seed production areas the following procedures will be followed:

a. 10 trees per month will be cut (June to September).
b. observations will be recorded of phenological events such as growth stage, flower, conelet, and cone development.
c. 5 cones per tree will be collected, measured, and checked for floatation in water, kerosene and SAE 20 motor oil.
d. these cones will be retained in individual tree lots for drying, recording of cone opening and seed extraction, and germination test results.

Permanent flowering and cone observation stations will be established in several of these seed production areas and in an 11 year-old seedling seed orchard.

CONCLUSIONS

The production of viable seed by Honduras pines in Puerto Rico appears to be linked to a pronounced dry season which favors good pollen dispersal. The high elevation wet sites produce abundant female flowers throughout the year but male flowering is sporadic. When anthesis does coincide with female flower receptivity the continuously wet conditions often limit pollen dispersal. This results in a large number of first year aborted ovules - the characteristic "wings without seeds" (Bramlett *et al* 1977).

Studies in process are designed to develop a better understanding of the phenology of Honduras pine in Puerto Rico. The cone maturation process will be observed by a series of monthly cone collections and phenological observations throughout the island.

REFERENCES

Bramlett, D. L., E. W. Belcher, Jr., G. L. De Barr, G. D. Hertel, R. P. Karrfalt, C. W. Lantz, T. Miller, K. D. Ware, and H. O. Yates III 1977. Cone analysis of Southern Pines. Gen. Tech. Rept SE 13, USDA Forest Service, SE For. Exp. Sta. and SE Area S&PF, Atlanta, Ga. 28 pp.

Delwaulle, J. C. 1982. Seed production of Pinus caribaea. FAO For. Gen. Res. Inf. No. 11. p 55. FAO, Rome.

Dvorak, W. S. 1977. Status of the tree improvement programs for Pinus caribaea var. hondurensis in Fiji, Proc. Third World Cons. on For. Tree Breeding, Canberra, Australia.

Gallegos, Carl M. 1980. Flowering and seed production of Pinus caribaea var hondurensis - Results of a worldwide survey. Proc. IUFRO Symp. and Workshop on Genetic Improvement and Production of fast growing tree species. Aguas de Sao Pedro, Brazil.

Ibrahim, Sheikh 1977. Problems of seed production in moist tropical climates. Proc. Third World Cons. on For. Tree Breeding, Canberra, Australia.

Venator, C. R. and U. F. Marcias Sanabria 1973. A problem of empty seed in Pinus caribaea in Puerto Rico. Turrialba 23(2):236-238.

NEW DIRECTIONS AND PROBLEMS FOR TREE BREEDING IN THE TROPICS

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ABSTRACT

American southern forests and foresters have been basic resources for the establishment of industrial plantations in many tropical countries and for the development of tree breeding in several. Now, however, national priorities are changing towards rural and social forestry, with new opportunities and new constraints. The opportunities include new species (particularly multipurpose species) and unfamiliar environments (especially arid, semi-arid and degraded lands) while the problems include large populations of humans and cattle (with consequent excessive demands for fuel and fodder), uncertain land tenure (with limits on resource inputs) and inadequate professional and technical staff.

Traditional research steps are still required (choice of species and provenance; selection, progeny testing and propagation; seed or other propagule production) but appropriate breeding strategies must be simpler than those now adopted with industrial species. Continuing international support is required to increase national capability.

INTRODUCTION

It is 20 years since I earned my first dollar as a student tree breeder, 30 m up a slash pine tree at Harrison Experimental Forest, Gulfport, Mississippi, under the watchful and amused eyes of E.B. Snyder and F. Mergen. At that time few tree breeders were working in the tropics (Queensland, Kenya, the Rhodesias and South Africa) and industrial plantations (excluding Australia) occupied a few thousand hectares. Now there are 11.5 million ha of tropical plantations (pine, eucalypts, teak, *Gmelina* mainly), the planting rate is 1 million ha per year and some types of tree breeding programmes exist in at least 30 countries. Many of these activities are based on southern pines and American nationals or foreign tree breeders trained in the US. One example is the Zimbabwe pine breeding programme which includes *inter alia* 8 x 8 full diallel crosses without selfs and 8 x 24 or 8 x 27 factorial crosses of *Pinus elliottii* and *P. taeda* on 6 - 8 trial sites, now 7 - 10 years old (Barnes,* pers. comm.).

The International Union of Forestry Research Organizations Working Party S2.03-01 (Breeding tropical and subtropical species) has 280 members in 75 countries of which 50 are in the geographic tropics. The Working Party has held several meetings at which many tropical breeders participated (Florida, USA, 1971; Nairobi, Kenya, 1973; Brisbane,

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* Personal communication, R D Barnes, Commonwealth Forestry Institute Oxford University, England.

Australia, 1977; Aguas Sao Pedro, Brazil, 1980). The bulk of the work has concerned survival, growth rate, form and occasionally wood properties; breeding strategies have tended to follow the classical pattern of species and provenance trials, selection of superior phenotypes (plus trees, often only 20-50), creation of primary seed orchards, progeny testing (mainly open-pollinated) and restructuring of seed orchards (to form the so-called 1.5 generation). Working Party S2.03-13 (Breeding southern pines) has recently been established, led by Dr. F. Bridgwater; this will have many tropical members.

Latterly some countries have entered phases of advanced generation breeding (e.g. Australia, Fiji, Zimbabwe with tropical pines); others have developed more advanced operational techniques such as rooted cuttings to capture specific combining ability superiority (e.g. Brazil, Congo, with tropical eucalypts) while some, usually twinned with an institution in a temperate country, are examining tissue culture as a means of propagation and genetic conservation (India, teak; Malaysia, oil palm; Nigeria, obeche - Triplochiton scleroxylon.) Opportunities for further improvement clearly exist in these approaches to commercial plantation species. However, in most tropical countries plantation forestry has given way to rural development forestry as a priority subject of investigation and investment; the object of this paper is to review the part that tree breeding may play and the problems that will be encountered.

The use of the one word "tropics" implies a uniformity that does not exist. The belt around the earth between 23.5° north and south of the equator contains ranges of vegetated altitudes (0-4,000 m a s l), vegetation types (evergreen rain forests to desert scrub), annual rainfall totals (0-10,000 mm), annual rainfall distributions (continuous to 1-2 months per year), soils (pH 3-9), densities of populations of humans and domestic animals, availabilities of professional and technical staff, skills and experience, and commitments by Governments to forestry.

RECENT TRENDS OF FORESTRY IN TROPICAL DEVELOPMENT

The importance of commercial plantations as contributors to economic development will of course continue in many tropical countries. However, it has recently been realised that these do not necessarily provide benefits that trickle down to rural populations. The World Bank (1978) revised its forestry sector policy to place investment in rural welfare ahead of industrial investments and most other development banks, multilateral agencies, bilateral donors and non-governmental organizations now follow similar policies.

In 1980-81, together with J. Spears and J.E.M. Arnold, I conducted a review of forestry research needs in developing countries for the preparation of a statement by World Bank and FAO (1981) to the 17th IUFRO Congress and the priorities have been widely accepted by donor and recipient organizations; they have led to the appointment by IUFRO of a special coordinator for developing countries. The broad subject priorities are:-

(i) Forestry in relation to agriculture and rural development
(ii) Forestry in relation to energy production and use
(iii) Management and conservation of existing resources
(iv) Industrial forestry

Tree breeding is identified in (i), (ii) and (iv) while genetics is implicit in (iii) so tree breeders can be assured of gainful employment in increasing numbers during the foreseeable future but their objectives will be very different from those encountered in industrial, temperate forestry

BENEFITS OF NON-INDUSTRIAL TREES AND FORESTS

In the rural situation the products and services obtained from trees are commonly in the reverse order of priorities compared with industrial plantations, namely site improvement, habitat improvement and production.

Site improvement includes soil or sand dune stabilization, protection of soil and water supplies, soil improvement (stucture, chemistry, water balance), and control of weeds.

Habitat improvement includes the provision of shade and shelter for humans, domestic animals and wild animals, and shelter for crops. In some countries amenity, tourism and recreation may be legitimate national objectives though they are less important at the level of local communities.

Products required rurally include poles, saw timber, fuel (mainly wood and charcoal), food for humans and domestic animals, other animal products (*e.g.* honey, silk) and chemical derivatives (*e.g.* essential oils, drugs, soaps).

The urgent need for these benefits can be seen from the following selection of global estimates based on various FAO and World Bank studies and on the report by Wood, Burley and Grainger (1982) for the US Congress Office of Technology Assessment:-

World area of closed forests	2860 million ha
Tropical area of closed forests	1160 million ha
Tropical area of moist forests	1060 million ha
Tropical humid deforestation	6 million ha per year
Arid/semi-arid deforestation	20 million ha per year agricultural lands and 4 million ha per year open woodlands
Desertification	affects 3000 million ha, 67% of the world's countries, and 17% of the world's population

Soil erosion following deforestation cost approximately US $ 1 million in India alone over the last three years and soil is Nepal's major export (1 billion tons annually). Forests moderate water flow and deforestation has contributed to shortages of drinking water in many large cities (*e.g.* Bogota, Jakarta, Kuala Lumpur, Lagos, Manaus, San Jose) while Bangkok is sinking faster than Venice as ground water is being pumped up to meet dry season needs that were formerly met by monsoonal rain water released slowly by upland forest areas. Reforestation rates approach 1 million ha per year of which half are industrial, the remainder meeting less than one fiftieth part of rural needs (*inter alia* the fuelwood deficit in arid and semi-arid lands requires the equivalent of 26 million ha of pure plantations, although the needs must be met by single trees in farm boundaries as much as by village woodlots). USAID is currently helping many countries with fuelwood projects (for some of which expatriate experts are required) and it is co-sponsoring fuelwood workshops with IUFRO in Africa and Asia.

SPECIES AND LANDUSE SYSTEMS TO PROVIDE THE BENEFITS

For any given site a wide range of species could possibly provide a given benefit. However, it is unlikely that trees or forests will be grown for a single benefit in rural locations. Both individual farmers and village communities, particularly those in areas of severe land pressure, require several benefits from one tree or plot. This introduces the recent (jargon) concepts of multipurpose trees and agroforestry systems.

Virtually all trees can be used for at least two purposes since they can be burned as well as used in solid form but multipurpose trees are difficult to define exactly; in common opinion they are species that can provide several products and benefits from the one tree, e.g. Azadirachta indica (Meliaceae) which can supply wood, fuel, chemicals, cattle fodder and shade (see Radwanski, 1977; Schmutterer, Ascher and Rembold, 1981), or Leucaena leucocephala (Leguminoseae) which can fix nitrogen, stabilise soil, and provide fodder, fuel and shade (NAS, 1977). Although recent attention has been concentrated on a few outstanding species such as the two above and several Acacia and Prosopis species many others have potential for different sites; the ICRAF/IBPGR/CFI/NAS workshop that preceded this meeting identified some 2000 species that have been recommended by someone for somewhere (see Burley, 1983) and the USDA Plant Genetic Resources Laboratory at Beltsville, Maryland, maintains a computer-based data bank on 1000 woody legumes most of which have at least nitrogen fixation and wood or fodder production as multipurpose attributes (see e.g. Duke, 1981). These large numbers immediately pose the problems of seed sources (exploration, taxonomy, supplies and certification) and comparative field trials. Agencies such as CFI, NAS and USAID that conduct exploration, conservation and evaluation of multipurpose trees were described in Burley (1983) and the workshop attempted to identify mechanisms for stimulating and coordinating internationally the necessary research and development of these species.

With increasing populations land pressure becomes intolerable and man's needs to have to be met from smaller areas of land. Agricultural crops, domestic animals and trees may be raised on the same plot, either in intimate spatial mixture or in temporal sequence. Such combinations are collectively called agroforestry (Lundgren, 1982) which is a land use system well suited to meet social and community forestry objectives (Burley and Wood, 1983). Agroforestry imposes unfamiliar constraints on the silviculturist. Experiments must be designed to include mixtures of annual and perennial crops, various spacings, unusual silvicultural treatments such as coppicing and pollarding, and the determination of yields and qualities of products other than the familiar stem wood (e.g. leaves, thorns, branches, extractives, palatability, burnability, etc.) A manual of methods for agroforestry research is in preparation by ICRAF and CFI with NAS support to amplify the manual on species and provenance testing for tropical plantation crops (Burley and Wood, 1976).

PROVENANCE

Many of the participants at this meeting deal with selective breeding of indigenous species for which either local origins are best or the stage of provenance trials is long past. It would be interesting to count how many here have actually designed or assessed a provenance trial. No doubt many work in cooperative organizations that exchange improved genetic material from a range of natural origins and I wonder if I dare ask if origin records are maintained for such material even though the natural range and variation are well known.

In contrast, for the species of use in the tropical rural scene, little is known about the natural range nor about the degree of genetic change caused by human activities such as selective or complete logging. Where trees have been planted the local source has usually been used and considerable land race differentiation has occurred. The importance of genetic history of both natural and derived provenances is well known (see Jones and Burley, 1973) and the place of provenance material in breeding strategies will be discussed in detail at the meeting of IUFRO Working Parties S2.02-08, S2.03-01 and S2.03-13 in Zimbabwe during April, 1984.

OBJECTIVES OF BREEDING

As introduced above, for many aspects of rural development multipurpose trees will be used and the principal objectives of breeding will be to increase the yield of their particular benefits or products. This will entail development of rapid assessment techniques for characters as diverse as nitrogen-fixation capacity, leaf palatability or alkaloid content, shade/shelter microclimatic effects, or soil holding ability in addition to standard wood or total biomass production.

The second set of objectives will be to yield seed or propagules that can be managed in small nurseries or by individual land owners who have little skill, resources or time for tree planting and maintenance or who often have little appreciation of the benefits likely to accrue. Since the individual farmer himself is not likely to practise tree breeding, particularly if his first plantings flower and seed early and prolifically, any improved planting stock must be provided cheaply by governmental and non-governmental organizations. It must obviously be backed up with agri-silvicultural research to determine crop mixtures and managerial practices and by extension services to publicise the benefits of using improved material and the methods of growing it.

A third set of objectives for many species may be the conservation of genetic variation by representatives of both natural populations and local land races. At present in forestry there is no equivalent of the international agricultural research institutes and other centres that maintain gene banks of many thousands of agricultural crop selections. Although some international agencies maintain samples of seed from several populations of some species, it is necessary for individual national organizations to create and maintain local gene pools for breeding for future changes of site, management, market, pests and diseases. Few have done this for species used in smallholder and community forestry.

CONSTRAINTS ON BREEDING

To meet rural land use objectives there are several constraints on breeding even a single species, assuming that information is available on the optimum species and provenance for each of the major products or benefits.

The first is the multiplicity of benefits itself which requires the derivation of selection indices and possibly the maintenance of multiple populations (see Namkoong, Barnes and Burley, 1980).

The second is the existence of genotype-environment interactions in which environment includes different sites, managerial methods, and agricultural crops if used in an agroforestry mixture. The range of contributing factors is large and the reduction of overall heritability and gain could also support the need for multiple populations.

The third is simply the cost of the research necessary to examine all combinations of site, species, management and benefit, and to develop appropriate populations. In many countries forestry has a low governmental priority within forest departments. This situation may be improved if donor funding supports research in rural forestry specifically and extension work generally.

Fourthly, tree breeding in tropical regions is constrained by inadequate staff numbers and skills. Many professional breeders have been trained in US universities but too often they are diverted to administrative or political office in national or international organizations. Until the market is saturated with qualified personnel one approach is the intensive specialised short courses such as those offerred periodically at CFI, Oxford or NC State University, Raleigh, and possibly in future by the South-East Consortium for International Development (Chapel Hill, NC). Further, donor agencies such as USAID can support the provision of American nationals either as Peace Corps volunteers or specialists on regular assistance projects in developing countries. A major factor in the success of all such projects is continuity and follow-up; rarely does a 2- or 3- year assignment achieve significant results and nowhere is this more apparent than in long-term activities such as tree breeding. An extended commitment of staff and institutional support is desirable and this can be obtained through the concept of twinning between institutions in developed and developing countries.

The first two of these constraints lead towards complexity of breeding strategy; the last two impose simplicity. Clearly a balance has to be struck for each country but in general appropriate strategies will be simpler than those currently operated in temperate regions.

REFERENCES

BURLEY, J. (1983). Background document for ICRAF/IBPGR/CFI/NAS workshop on multipurpose tree germplasm, Washington, DC, USA. ICRAF, Nairobi, Kenya, 70p and 18 appces.

BURLEY, J. and WOOD, P.J. (1976). A manual on species and provenance research with particular reference to the tropics. Trop. For. Pap. Commonw. For. Inst., Oxford, England, No. 10, 226p.

BURLEY, J. and WOOD, P.J. (1983). Development of curricula for community forestry. Pap. Twelfth Sess., FAO Adv. Cttee. For Educ., Nairobi, Kenya. FO: ACFE - 83/12, FAO, Rome, Italy, 6p.

DUKE J.A. (1981). Handbook of legumes of world economic importance. Plenum Press, New York, USA, 345p.

JONES, N. and BURLEY, J. (1973). Seed certification, provenance nomenclature and genetic history in forestry. Silvae Genetica 22(3), 53-8.

LUNDGREN, B. (1982). The use of agroforestry to improve the productivity of converted tropical land. Rept. US Congr. Office of Technology Assessment, Washington, DC, USA, 81p.

NAMKOONG, G., BARNES, R.D. and BURLEY, J. (1980). A philosophy of breeding strategy for tropical forest trees. Trop. For. Pap. Commonw. For. Inst., Oxford, England, No. 16, 67p.

NAS. (1977). Leucaena - promising forage and tree crop for the tropics. National Academy of Sciences, Washington, DC, USA, 115p.

RADWANSKI, S. (1977). Neem tree. I. Commercial potential, characteristics and distribution. World Crops and Livestock, March/April, 62-6.

SCHMUTTERER, H., ASCHER, K.R.S. and REMBOLD, H. (eds). (1981). Natural pesticides from the neem tree (Azadirachta indica A. Juss). Proc. First Intl. Neem Conf., Rottach-Egern, Germany. GTZ, Eschborn, Germany, 295p.

WOOD, P.J., BURLEY, J. and GRAINGER, A. (1982). Technologies and technology systems for deforestation of degraded tropical lands. Rept. US Congr. Office of Technology Assessment, Washington, DC, USA, 114p.

WORLD BANK. (1978). Forestry: sector policy paper. World Bank, Washington, 68p.

WORLD BANK and FAO. (1981). Forestry research needs in developing countries - time for a reappraisal? Spec. Pap. 17th IUFRO Congr., Kyoto, Japan, 56p.

ADVANCES IN SEED ORCHARD MANAGEMENT

.GEOGRAPHIC LOCATION AFFECTS FLOWERING OF LOBLOLLY PINES

R. C. Schmidtling[1]

Abstract.--Loblolly pine seedlings and grafts were planted in four locations: south Florida, north Florida, south Mississippi, and north Mississippi. Male and female flowering were measured each year for 6 years. Grafts and seedlings flowered first in the south Florida planting. Flowering in all plantings was inversely proportional to latitude through the fourth year, i.e., the plantings in order of fruitfulness were south Florida > north Florida > south Mississippi > north Mississippi. After age 4, flowering was best at the north Florida planting, possibly because of better site and management.

The tendency for more southern orchards to flower earlier is confirmed, although orchard site quality and management were also important.

Early and abundant flowering can greatly enhance production of improved seed and shorten breeding generation intervals in southern pine tree-improvement programs. Thus it is important to determine the extent of locational effects on flowering and seed production for use in selecting locations for future seed orchards.

Evidence has accumulated (Schmidtling 1977, 1979, Gansel 1973) that geographic location can strongly affect flowering in southern pines. Flowering and seed production seem to be greater in southern locations when compared to northern locations (Sarvas 1970, Werner 1975).

The objective of this study is to determine the extent of geographic variation in flowering of loblolly pine seedlings and grafts. Seedlings as well as grafted loblolly pines were included in this study to examine two different but closely related aspects of flowering: (1) will location affect the quantity of flowers and seeds produced in reproductively mature trees, and (2) will location affect the age of first flowering in seedlings ("ripeness to flower").

MATERIALS AND METHODS

The experimental plantings were established using grafts of 10 loblolly pine clones and also seedlings from 5 of the same clones. Scions from the 10 scion clones varying widely in flowering potential were collected from ramets located in the Erambert Seed Orchard in south Mississippi and grafted on potted seedling rootstocks in January of 1977. Original ortets were located in south and central Mississippi (fig. 1).

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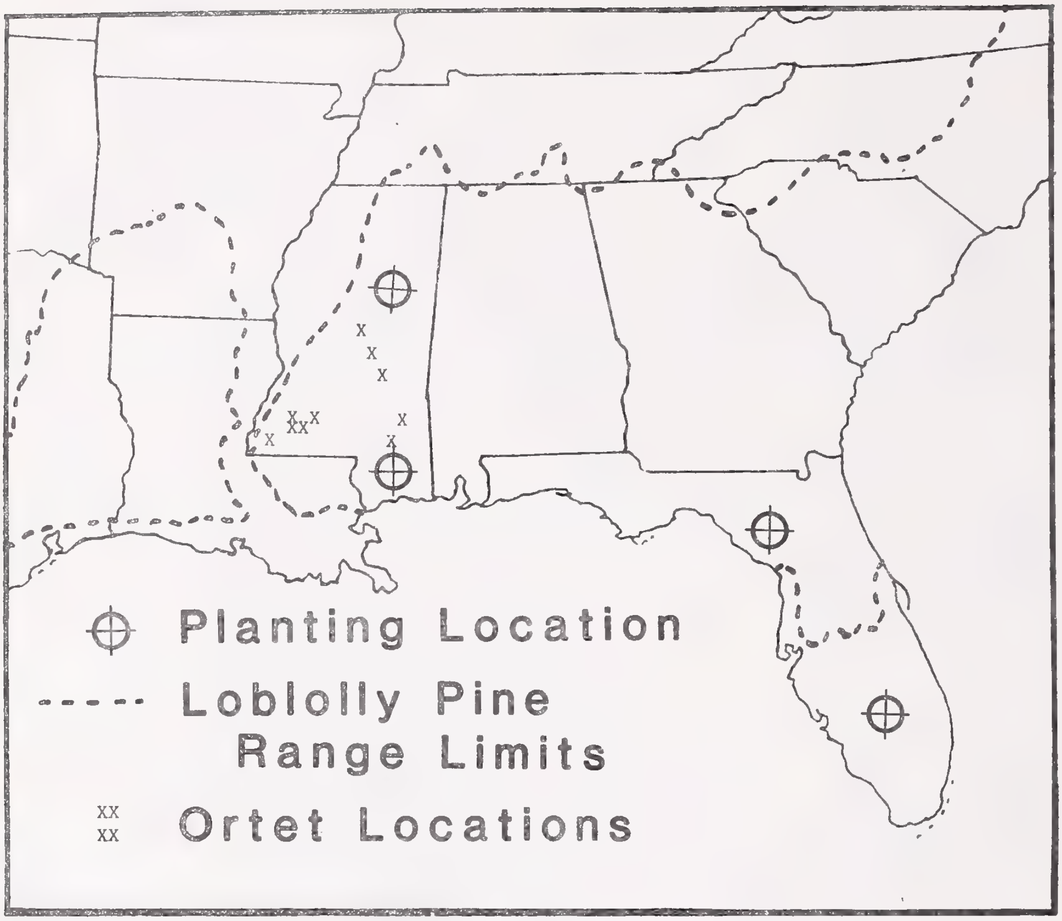

Figure 1.--Map of southeastern United States showing the planting locations, the locations of the original ortets used for grafts and seedlings, and the botanical range limits of loblolly pines (adapted from Critchfield and Little 1966).

Five successful grafts of each scion clone were outplanted as single-tree plots at each location in June of 1977. Five potted seedlings from each of five families were also outplanted, for a total of 75 trees at each location (50 grafts + 25 seedlings). Trees that died the first season were replaced in March of 1978 with potted grafts and seedlings of the same age that were held for that purpose in a lath house at the Harrison Experimental Forest in South Mississippi.

The planting locations (fig. 1) vary not only in latitude but also in site quality (table 1). The south Florida planting is in Glades County, located in what was formerly a pasture but is now planted in eucalyptus. The site is poorly drained and has been bedded, with rock phosphate applied to correct a phosphate deficiency. There has been no maintenance other than the initial site preparation.

The north Florida planting is contiguous to a producing seed orchard, and receives the same care as the orchard. It is consequently in excellent condition.

The south Mississippi planting is located on the Harrison Experimental Forest. It has been mowed for competition control annually, but has received no other treatments.

The north Mississippi planting is located on a fertile but poorly drained site. It has also been mowed annually, but has received no other treatments.

Table 1.--Site characteristics and survival data for the four planting locations

Location	Latitude	Soil Series/ Surface Texture	Drainage	6th-year survival grafts	6th-year survival seedlings
	---°N---			---------%---------	
South Florida	27.1	Myacca Fine loamy sand	Poorly to somewhat poorly	50	80
North Florida	29.6	Lake Fine sand	Well	96	100
South Mississippi	30.5	Saucier Fine sandy loam	Moderately well	98	96
North Mississippi	33.3	Urbo Silty clay loam	Poorly to somewhat poorly	38	44

Female strobili and male strobili clusters were counted and their heights measured each year. Flowering data from the seedlings were handled as a qualitative trait, i.e., either the seedlings flowered or they did not. Flowering indicates reproductive maturity or "ripeness to flower." The ripeness to flower concept assumes that once flowering occurs, it is not reversible (Schmidtling 1981), even though flowering may not occur in subsequent years. Proportion of total trees flowering was arc-sine square root transformed for analysis.

Flowering data for grafts was handled as a quantitative trait. Counts were square-root transformed for analysis. Analysis of variance was used to compare location and clone means. Differences were tested at the 0.05 level of probability.

RESULTS AND DISCUSSION

Survival of trees planted at the two mid-latitude sites, north Florida and south Mississippi, was excellent, ranging between 96 and 100 percent for both seedlings and grafts (table 1). Survival in the northernmost and southernmost plantings was not as good. The same two factors adversely affected survival in both plantings: poor drainage and animal damage. In south Florida, many trees were trampled by cattle; in north Mississippi damage was caused by some unknown animal, perhaps beavers, stripping bark from the trees. In addition, the south Florida planting suffered from lack of competition control. In spite of poor survival, all 10 clones and 5 families were represented at all locations.

For the first 3 years, female flowering conformed to the expectations that the more southern plantings would flower better (fig. 2). Flowering of grafts commenced the first year after planting in south Florida, although the differences were not statistically significant (Fig. 2a). Flowering was best in the south Florida planting and second best in the north Florida planting through the third year. The fourth year (1981) there was essentially no flowering. At age 5, flowering in the north Florida planting equaled the south Florida planting; by age 6 the north Florida planting greatly exceeded the south Florida planting, when the grafts averaged 31 female strobili in north Florida vs 8 female strobili in south Florida.

There was very little flowering in the south Mississippi planting until the fifth year (fig. 2a). Flowering was consistently poor in the north Mississippi planting, and there were no female strobili at all the sixth year of the study.

In the statistical analyses, location effect was very strong. Clone effects, though significant, were much smaller. Location x clone interaction was not significant. This was not expected. In previous flower induction experiments, clonal effects were very strong, and clone x treatment interactions were significant (Schmidtling 1974).

Female flowering of the seedlings closely paralleled flowering of the grafts, although flowering did not begin until the third year (fig. 2b), when 33 percent of the south Florida seedlings flowered and 4 percent of the north Florida seedlings flowered. None of the seedlings in the other plantings flowered until age 5. By age 5, the north Florida seedlings exceeded the south Florida seedlings in "ripeness," and by age 6, 92 percent of the north Florida seedlings had flowered, compared to 72 percent in south Florida, 53 percent in south Mississippi, and 10 percent in north Mississippi.

Light and sporadic male flowering occurred on grafts in south Florida the second and third year, and none in the other three plantings. The pattern among locations for male flowering was similar to that for female flowering. At age 6, grafts and seedlings in north Florida averaged 5.8 pollen clusters per tree and 14.7 clusters per tree, respectively. Grafts and seedlings averaged 0.5 and 2.6 clusters per tree, respectively, in south Florida. There were only a few male strobili clusters at the other two locations.

Management and site conditions of the north Florida planting undoubtedly account for much of this planting's superiority in flowering in later years. The north Florida planting was fertilized along with the adjacent production orchard, and the site is well drained and more suitable for pines than the South Florida site.

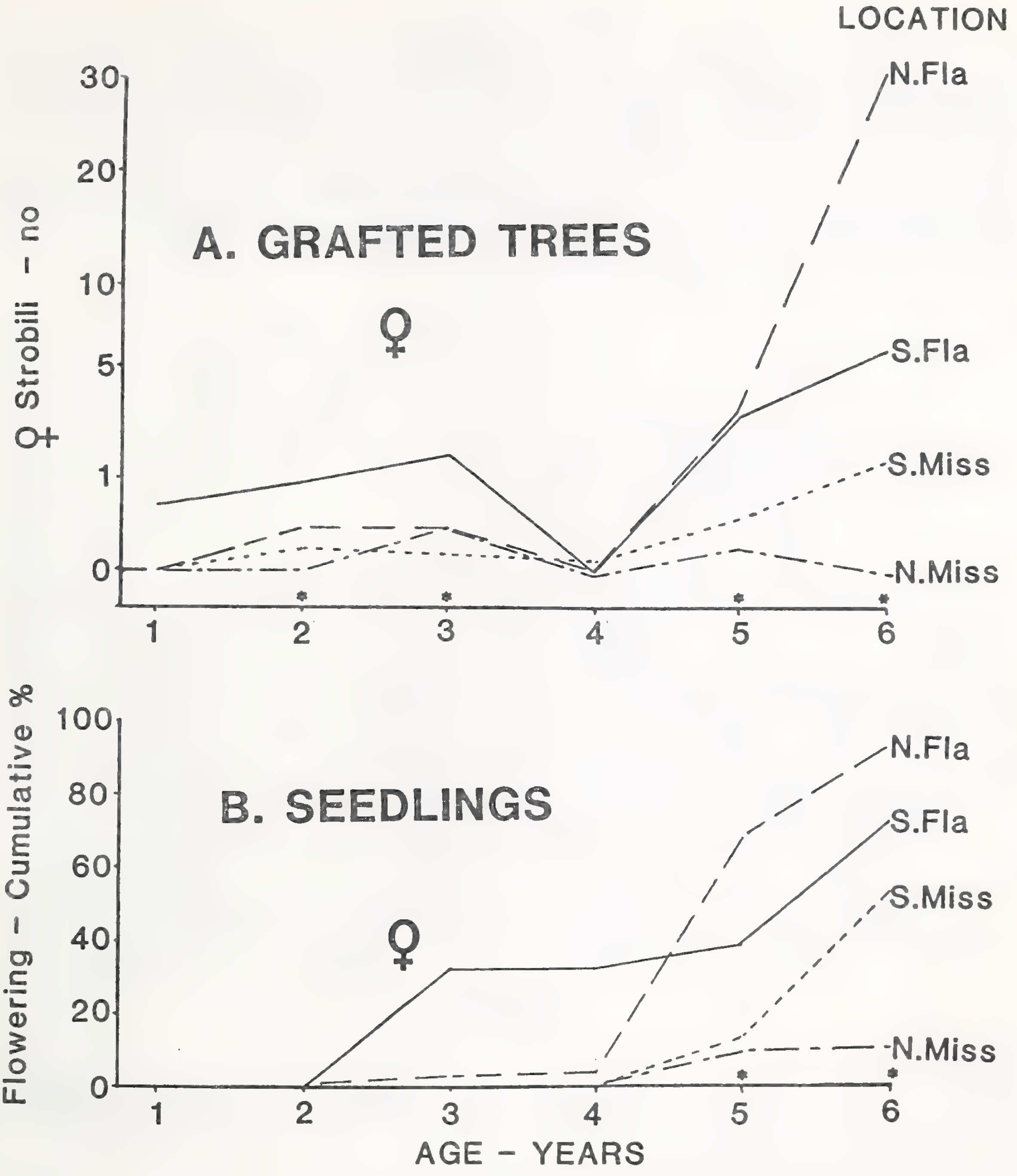

Figure 2.--Female flowering of grafted and seedling loblolly pines planted in four locations. Data recorded over 6 years. Vertical axis of (A) is square-root scale. *indicates that location differences for that year were statistically significant.

The superior management and site are evident in the size of the trees, as the seedlings and grafts in the north Florida planting were taller at age 6 than those in the other three plantings (fig. 3). But size alone cannot account for differences in flowering. The grafts in north Mississippi were nearly as tall as those in north Florida, and the seedlings in north Mississippi were second in height among the four plantings, yet flowering was consistently poorest in north Mississippi. Also, grafts and seedlings in south Florida are the shortest of all four plantings, but flowering in south Florida ranges from best to second best.

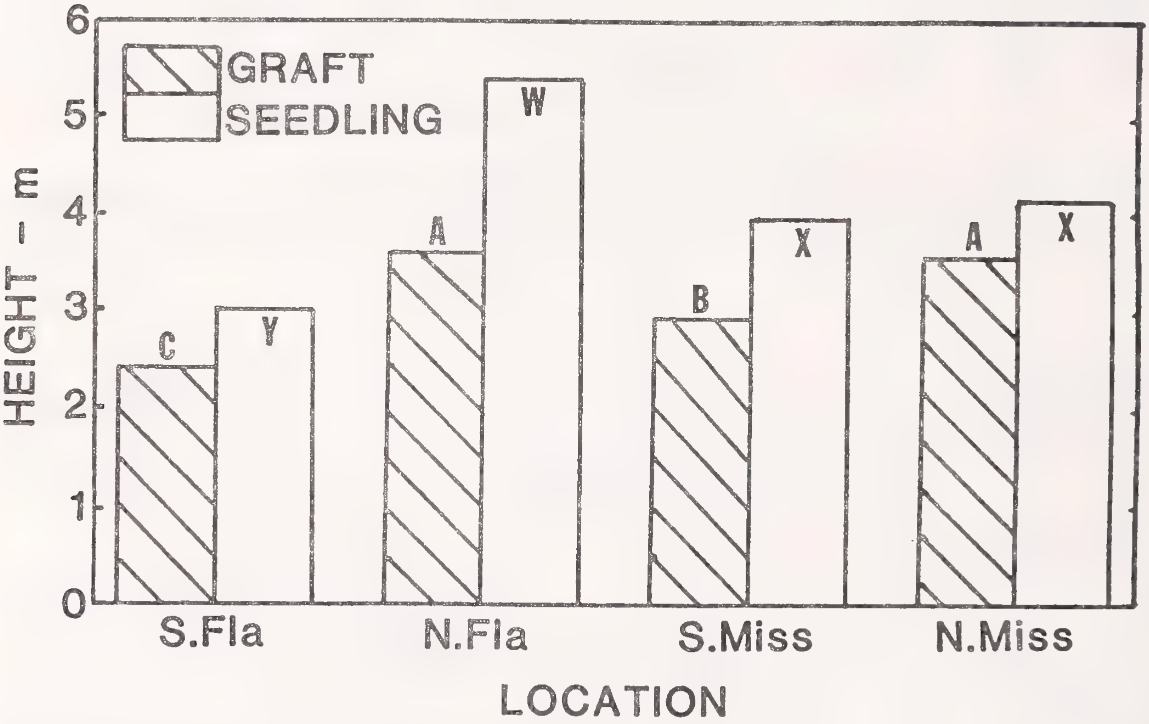

Figure 3.--Height of grafted and seedling loblolly pines planted in four locations after 6 years in the field. Bars topped by the same letter do not differ significantly according to Duncan's multiple range test (seedlings and grafts analyzed separately).

CONCLUSIONS

The results of this study support the observations that orchards sited in more southerly locations have a tendency to flower better. It is also clear that site and management are at least as important as location. Site quality was confounded with location in this study but it is interesting that the south Florida planting, where maintenance and growth were poorest, ranged from best to second best out of the four plantings in flowering. A better site with good maintenance in south Florida might have yielded consistently superior results across all years.

LITERATURE CITED

Critchfield, W. R., and Little, E. L., Jr. 1966. Geographic distribution of the pines of the world. U.S. Dept. Agric. For. Serv. Misc. Pub. 991. 97 p.

Gansel, C. R. 1973. Should slash pine seed orchards be moved south for early flowering? In 12th South. For. Tree Improv. Conf. Proc., p. 310-316.

Sarvas, R. 1970. Establishment and registration of seed orchards. Folia. For. Fenn. 89.

Schmidtling, R. C. 1974. Fruitfulness in conifers: Nitrogen carbohydrate, and genetic control. In 3rd North American Forest Biol. Workshop Proc., Ft. Collins, CO, p. 148-164.

Schmidtling, R. C. 1977. Movement of shortleaf pine seed orchards may greatly increase flowering. In 14th South. For. Tree Improv. Conf. Proc., p. 138-143.

Schmidtling, R. C. 1979. Southern loblolly pine seed orchards produce more cone and seed than do northern orchards. A symposium on flowering and seed development in trees. Proc. IUFRO Symposium, Starkville, Miss. 1978. p. 177-186.

Schmidtling, R. C. 1981. The inheritance of precocity and its relationship with growth in loblolly pines. Silvae Genet. 30:188-192.

Werner, M. 1975. Location, establishment and management of seed orchards. Pages 49-57 in R. Faulkner, ed. Seed orchards. For. Com. Bull. 54, London: H. M. S. O.

THIRD-YEAR SEED PRODUCTION IN OUTPLANTED SWEETGUM RELATED TO NURSERY ROOT COLONIZATION BY ENDOMYCORRHIZAL FUNGI

Paul P. Kormanik[1]

Abstract.--A sweetgum plantation was established from nursery seedlings grown in soil infested with vesicular-arbuscular mycorrhizal (VAM) fungi and amended with phosphorus at 25 ppm (Bray II); control seedlings were grown without VAM fungi and with soil P adjusted to 800 ppm. At the end of the third year, seed production was observed on 78 young trees, 75 from the VAM treatment and 3 from the control. In another plantation established from seedlings grown in VAM fungus-infested nursery soil and outplanted on a site that received different fertilization regimens with sewage sludge, heavy seed production was observed in both the fourth and fifth years. Observations in both plantations indicate that early seed production can be attributed to both VAM fungal root colonization and high levels of available soil P on the planting site.

Additional keywords: Vesicular-arbuscular mycorrhizae, early seed production, soil phosphorus, *Liquidambar styraciflua* L.

For practical purposes one can generalize that almost all plants require mycorrhizae to survive and grow in a natural environment. Most agricultural plants can be, and frequently are, fertilized with phosphorus and nitrogen compounds so that growth and yield are not noticeably improved by endomycorrhizae. In forestry, we cannot afford to apply high rates of fertilizer to maintain phosphorus above the soil phosphorus threshold level[2] for forest trees on routine forest sites; trees must rely on mycorrhizae to obtain needed nutrients. Trees with mycorrhizae will grow well in soils with phosphorus below the threshold level. In many forest soils, available soil phosphorus is so low that important tree species symbiotic with endomycorrhizal fungi would probably never become established in the absence of mycorrhizae (Marks and Kozlowski 1973, Kormanik and others 1977).

Fortunately, endomycorrhizal fungi are ubiquitous in nature and are well represented in natural forest soils. Because they are widespread, their importance has been underestimated or overlooked by many forest scientists. In the Southeastern United States forest soils seldom contain more than 10 ppm of available phosphorus (Bray II); most contain less than half this amount. In such soils endomycorrhizal fungi are indispensable to their tree hosts.

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[2] Soil phosphorus threshold level is that concentration of available soil phosphorus at which a nonmycorrhizal plant will grow as large as a mycorrhizal plant at the same phosphorus concentration.

Since 1975, scientists at the Institute for Mycorrhizal Research and Development (IMRD) in Athens, Georgia, have been investigating the importance of vesicular-arbuscular endomycorrhizal (VAM) fungi to growth and development of some of the more important commercial hardwoods. Initially, we were interested in determining whether VAM fungi benefit seedling production in hardwood nurseries by improving seedling quality similar to that found with ectomycorrhizal manipulation in pine nurseries (see Marx and others 1982). Early in the program it became apparent that the VAM technology developed in our experimental nursery had great potential for improving seedling quality of sweetgum (Liquidambar styraciflua L.) (Kormanik and others 1977).

In our early nursery experiments, we found significant and consistent improvement in growth of half-sib sweetgum seedlings from selected families if we maintained moderate levels of available soil phosphorus (25 ppm, Bray II) and had adequate VAM fungal inoculum in the nursery soil (Bryan and Kormanik 1977, Kormanik and others 1977). We were unable to test the performance of these seedlings on outplanting sites because of the great differences between the size of the VAM and the nonmycorrhizal seedlings.

After 5 years of testing we determined the phosphorus threshold level for sweetgum that enabled us to produce nursery-grown nonmycorrhizal sweetgum seedlings equal to or larger than VAM seedlings grown at low to moderate soil phosphorus levels. This threshold level is approximately 40 to 50 ppm of available P (Bray II) for sweetgum as well as for other selected hardwoods examined in our research. Sweetgum seedlings from most half-sib seedlots grown in soils below the threshold level needed VAM to develop beyond the primary leaf stage (Bryan and Kormanik 1977, Kormanik and others 1977). As available P exceeds this threshold level (up to about 250 ppm P) nonmycorrhizal seedlings grow well, but family growth response and root colonization by VAM fungi are often erratic.

Nursery experiments and outplanting trials are underway to determine family response when seedlings with and without VAM are grown at given increments above the phosphorus threshold level. Following leads developed in citrus research (Menge and others 1978), early in our program we increased P to very high levels and found we could grow large nonmycorrhizal seedlings when available soil P was approximately 800 ppm. These nonmycorrhizal seedlings were compared with VAM seedlings (i.e., those inoculated with selected VAM symbionts and grown in soil with 25 ppm P) in an outplanting experiment. Although this study will not be completed until after the fifth growing season (1984), observations of differences between treatments in early seed production are reported.

STUDY INSTALLATION

Seed were collected from four mother trees on the Scull Shoals Experimental Forest in northeast Georgia during the last week of September 1977. Two of the selections (77-14U and 77-12U) were growing on typical, infertile upland piedmont sites, and the other two (76-2B and 77-5B) were selected from fertile river bottom sites.

In May 1978, seed were sown in three nursery beds at the IMRD experimental nursery maintained at the University of Georgia's Whitehall Forest. Each bed (1.22 m x 18.3 m) contained 22.3 m^2 of forest soil which had been fumigated with methyl bromide (Dowfume MC-2). Two beds contained soil with available soil phosphorus standardized at 50 ppm; one was infested with the VAM fungus Glomus etunicatus and one with G. fasciculatus. The third bed was not inoculated and soil phosphorus was adjusted to 800 ppm. Each bed was divided into four equal compartments; each seed lot was randomly planted in a compartment. Seed were planted in 30 evenly spaced rows within each compartment for a final seedling density of approximately $60/m^2$ $(6/ft^2)$.

Beginning in May 1978, all seedlings were top dressed with a total of 560 kg/ha of nitrogen applied as NH_4NO_3 in 10 equal amounts of 56 kg/ha of N every 2 weeks. The beds were watered as needed throughout the growing season. Seedlings were lifted in late January 1979, measured, placed in cold storage, and outplanted by hand during the first week of February on a site at the Savannah River Plant near Aiken, South Carolina.

The study was installed on an upland piedmont site with a site index between 80 and 85 for loblolly pine (age 50). In 1974, a natural loblolly pine stand had been harvested from this site and natural vegetation consisting of grasses, hardwood sprouts, and dense thickets of blackberry (Rubus spp.), all of which are good host plants for VAM fungi, became established. In the fall of 1978, the site was prepared with a KG blade and root rake; debris was windrowed and the site double disked prior to planting. An assay of 20 soil samples, randomly collected from the site, revealed VAM fungal spore counts in excess of 3500/100 cc of soil.

The study had five blocks, each containing 12 plots (3 mycorrhizal conditions x 4 mother trees). Each plot was hand-planted to 25 permanent test trees spaced at approximately 3 m x 3 m (10 ft x 10 ft). An additional 15 seedlings per plot were planted approximately 0.3 m from preselected permanent test seedlings. Five of these extra seedlings per plot were excavated each year for 3 years to assess VAM development.

In April 1979, the study area was fertilized with 280 kg/ha of diammonium phosphate and was fertilized annually for three additional years with 280 kg/ha of ammonium nitrate. The plantation was disked three times during the first growing season, twice during the second and third growing seasons, and once, after fertilization, early in the fourth growing season.

RESULTS AND DISCUSSION

Initiation of flower buds was first observed at the end of the second growing season (January 1981). The swelling and characteristic shapes of the flower buds were noted, but no buds were removed and dissected. Staminate flowers were first observed in April 1981. We decided not to tag these flowering trees because we felt they would abort early in the growing season. In mid-July, we observed that some developing seedballs on these trees had aborted but others appeared to be developing as well as those from mature trees in the adjacent natural stand.

In late July 1981, 78 trees that had seedballs were tagged. Only three of these trees were from the nonmycorrhizal, high P nursery treatment. In early October, all tagged trees produced mature seed. We then collected seed from the original mother trees at the Scull Shoals Experimental Forest to compare germination percentages of these seed with those from the young, half-sib test trees. Only 30 of the 3-year-old seedlings produced 10 or more seedballs. The other 48 tagged seedlings produced less than five seedballs each. Since so few sound seed were produced on these trees, testing was restricted to those seed collected from the 30 trees bearing 10 or more seedballs (Table 1). In 1981, seed from the young 77-14U and 12U half-sib progeny germinated significantly better than the seed from their original mother trees. In 1978, seed from these same mother trees had germination percentages of 86 and 72, respectively. There were no significant differences in seed germination between the 76-2B and 77-5B half-sib progeny and their original mother trees. In 1978, seed germination percentages for these mother trees were 72 and 78, respectively.

Table 1.--Germination of seed collected from 3-year-old sweetgum half-sib progeny and original mother trees, 1981.

Family	Percent germination	
	Progeny	Mother tree
77-14U	96	72
77-12U	90	75
76-2B	79	75
77-5B	80	89

In January 1982, buds from more than 100 young trees in this plantation were sampled. Immature flowers were found in more than 30 percent of them, however, no seed production was recorded because a killing frost in late April destroyed all the flowers, as well as the 1982 sweetgum seed crop throughout the piedmont of Georgia and North Carolina. We did employ the same fertilization schedule (280 kg/ha NH_4NO_3 (250 lg/A) applied in April) for an additional year to improve chances for a good seed crop in 1983.

At the end of the first growing season, approximately 85 percent of all feeder root samples from the 180 seedlings excavated were heavily colonized by VAM fungi. Sampling of roots showed that it was not until late August that the initially nonmycorrhizal/high phosphorus seedlings had significant VAM fungal colonization. Therefore, these seedlings received no benefit from VAM until late in the first growing season. The fact that 75 of the 78 trees producing seed at the end of the third growing season had VAM at planting suggests that VAM affects host metabolic functions in sweetgum that can have lasting effects not currently recognized or, at least, poorly understood.

The presence of VAM only partly accounts for this stimulation of early seed production. In other plantations that we observed, seedlings with VAM at planting failed to produce seed even after 5 years in the field; however, additional P was not applied after planting. In another field study with sweetgum, sewage sludge was used as an amendment. After 5 years, evidence of heavy seed production during the fourth and fifth growing seasons was noted on trees growing in soil with 47 to 75 ppm available P. Apparently, levels of available P in the soil 4 to 8 times that normally found in nonamended soil (10 ppm) can have a direct effect on early seed production of sweetgum.

In this present study, 30 to 35 ppm available P was applied in 0.75 to 1 m (2 to 3 ft) width bands (ca 60 lb/A of available P) when the trees were initially fertilized. This means of application provided considerably more than 30 to 35 ppm available P in the immediate root zone of seedlings. After the third growing season, assay of soil samples showed that 30 ppm P (Bray II) was available in a 1-m circle around the trees. We have not observed early seed production in any of our young sweetgum plantations where soil phosphorus is below 10 ppm.

In April 1983, just 2 weeks before the two killing frosts of April 18-19, we examined all trees in this plantation for flower development. All trees were equally well colonized by VAM fungi during the entire growing season in which flowers were initiated. As yet there is no assessment of the possible frost damage, but before the frost there were no differences in flower production based upon the initial nursery treatments.

It is commonly recognized that sweetgum seed orchards are not nearly as productive as they need to be. Observations over the past 3 years suggest that, perhaps, seed orchard fertility trials should be established to clarify the role of soil phosphorus availability and seed production for this species. The soil phosphorus levels should not be so high that they interfere with or reduce the mycorrhizal dependency of the selected trees. This type of research is well within the capabilities of our present VAM technology and should be encouraged.

Seedlings characteristically grow slowly during the first 3 or 4 years in sweetgum plantations on upland sites. Increment growth in this study, however, has been excellent. At the end of the fourth growing season the average height was more than 3 m (9 ft) and the average DBH was ca 3.5 cm (1.4 inch); lateral branches of adjacent rows were frequently touching along the lower 1.5 m (4.9 ft). Crown closure should occur sometime during the fifth growing season. This is remarkable growth when one considers that during the first 2 years of plantation establishment this area experienced the two driest years on record. In the second year, less than 7 inches of rain fell on the site from mid-May until the end of August. We feel strongly that the plantation performance is correlated with the exceptionally high levels of mycorrhizal spores in the soil that were available for rapid and effective root colonization. Spore levels were 10 to 20 times greater than what we normally observe in cutover forest stands. Undoubtedly, the high spore level can be attributed to the clearcut and revegetation by VAM plants during the 4 years that the site lay fallow. During this fallow period the plant succession was primarily plant hosts that stimulated the VAM fungal populations.

Also, it should be noted that this plantation was cultivated more than is normal in an operational outplanting. Extra cultivation was needed to allow seasonal excavation of seedlings and assay of roots for infection by VAM fungi. During excavation we noted that cultivation enhanced lateral root development. Many roots damaged by cultivation tended to develop massive, fan-shaped clusters of feeder roots. Closer examination of these new roots showed that they were well colonized with VAM fungi. This additional root development certainly improved nutrient water uptake.

Another interesting observation was that newly planted sweetgum seedlings do not initiate significant new root growth until the leaves are fully expanded in late June or early July. The same pattern of root growth has been observed in three other plantations recenly established. It appears, therefore, that intact and functional roots on planting stock must sustain the newly planted seedling until at least midsummer.

We have concluded that VAM development on seedlings at planting, high levels of available P in soil, and cultivation during the early years of plantation establishment may affect precocious seed production in sweetgum.

LITERATURE CITED

Bryan, W. C., and Kormanik, P. P. 1977. Mycorrhizae benefit survival and growth of sweetgum seedlings in the nursery. South. J. Appl. For. 1: 21-23.

Kormanik, P. P. 1981. A forester's view of vesicular-arbuscular mycorrhizae and their role in plant development and productivity. In Mycorrhizal associations and crop production, p 33-37. N.J. Agric. Exp. Stn., Res. Rep. No. R04400-01-81.

Kormanik, P. P., Bryan, W. C., and Schultz, R. C. 1977. Influence of endomycorrhizae on growth of sweetgum seedlings from eight mother trees. For. Sci. 23:500-506.

Marks, G. C., and Kozlowski, T. T. (eds.). 1973. Ectomycorrhizae—Their ecology and physiology. Academic Press, New York and Canada. 444 p.

Marx, D. H., Ruehle, J. L., Kenney, D. S., [and others]. 1982. Commercial vegetative inoculum of *Pisolithus tinctorius* and inoculation techniques for development of ectomycorrhizae on container-grown tree seedlings. For. Sci. 28:373-400.

Menge, J. A., Labanauskas, C. K., Johnson, E. L. V., and Platt, R. G. 1978. Partial substitution of mycorrhizal fungi for phosphorus fertilization in the greenhouse culture of citrus. Soil Sci. Soc. Am. J. 42:926-930.

PINE WILT AND PITCH CANKER OF VIRGINIA PINE IN SEED ORCHARDS

L. David Dwinell and Jane Barrows-Broaddus[1]

Abstract.--Decline and mortality of Virginia pines in seed orchards is emerging as a major problem. Pitch canker, pine wilt, and declining root systems appear to be responsible for the mortality. Factors that cause a stress in Virginia pines in seed orchards contribute to the increased susceptibility of trees to these diseases. Research is needed to determine the role each of the diseases plays in tree mortality, to ascertain the influence management practices have on disease incidence, and to develop control stratagies.

Additional keywords: Fusarium moniliforme var. subglutinans, Bursaphelenchus xylophilus, root rot, wounds, resistance, control

Virginia pine (Pinus virginiana Mill.) occurs naturally from central Pennsylvania and New Jersey southward to Alabama (Box and Foil 1968), and is grown for pulpwood on 25 to 35-year rotations throughout its natural range. However, this species is known for persistent limbs which makes it undesirable to pulpwood cutters (Williston and Balmer 1980). Conversely, these characteristics plus short, dark green needles, make it suitable for Christmat trees (Box and Foil 1968). Plantings of Virginia pine Christmas trees in the Southeastern United States have increased dramatically since 1970, and the species is now a serious competitor in regional markets (Murray et al. 1981; Utz and Balmer 1980).

At present there are approximately 235 acres of Virginia pine seed orchards in the southern United States (Anonymous 1982), with some orchards supplying genetically improved seed to the Christmas-tree market (Chandler 1979). The seed orchard environment differs considerably from those under which the species has been grown in the past, and that environment is proving conducive to the emergence of new insects and disease problems and the resurgence of old ones (Gibson and Jones 1976; Shea 1971). Two previously endemic diseases of this species, pitch canker and pine wilt, currently threaten Virginia pines grown in seed orchards.

The pinewood nematode, Bursaphelenchus xylophilus (Steiner & Buhrer) Nickle, causes a wilt disease of pines (Nickle 1981). Although the disease is epidemic on pines in Japan, it is apparently endemic in the United States (Dropkin et al. 1981). The nematode is vectored primarily by longhorn beetles (Coleoptra: Cerambycidae) that emerge from dead trees carrying the dauer larvae. When the beetles feed on healthy trees, the resulting wounds provide points of entry for the nematode larvae. The nematodes mature and reproduce rapidly in the resin canals, reducing oleoresin flow, arresting transpiration, and causing chlorosis and death within 3 months after initial infection. The beetles oviposit in dying trees, and the life cycle of the nematode, closely coordinated with the beetle, is repeated (Dropkin et al. 1981; Wingfield et al. 1982). By December 1980, the pinewood nematode has been recovered from Virginia pines in Illinois, Indiana, Maryland, South Carolina and Virginia (Dropkin et al. 1981).

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Pitch canker, caused by *Fusarium moniliforme* Sheld. var. *subglutinans* Wr. & Reink. (Kuhlman et al. 1978), was first reported on Virginia pine in 1946 (Hepting and Roth). Virginia pine is now ranked as one of the most susceptible species to this disease (Dwinell 1978; Barrows-Broaddus and Dwinell 1979). The cankers, which occur primarily on the bole and main branches, are sunken and characterized by heavy pitch flow and by resin soaking of the underlying wood (Hepting 1954). The causal fungus can invade any fresh wound, regardless of cause or location (Blakeslee et al. 1980; Dwinell and Barrows-Broaddus 1981).

PINE WILT

In the past 18 months, we have been asked to examine two Virginia pine seed orchards in which the trees showed a sudden loss of normal leaf coloration, turned a bright rust red, and rapidly died. Initially, the problem had been diagnosed as pitch canker. Although the symptoms of pitch canker were apparent, and the causal fungus was isolated, the incidence of pitch canker in the orchards could not alone explain the sudden and extensive mortality. Furthermore, the slight degree of resin-soaking of the sapwood beneath the cankers was atypical of pitch canker on Virginia pine (Hepting 1954). In the past, mortality of Virginia pines in seed orchards caused by pitch canker has averaged 4-5% per year (Dwinell and Barrows-Broaddus, unpublished). As of December 1982, mortality averaged 30% at the Champion International (Newberry, S. C.) and Hammermill (Selma, Al.) seed orchards.

Trees were exacavated at both locations because the sudden decline of Virginia pine suggested that the problem might be in the root systems. At the Hammermill orchard, where Virginia pine is used as the root stock, three of the four declining trees that were excavated had deteriorated root systems. The root systems exhibited nonspecific, general decay. Symptoms and signs of root rots caused by *Heterobasidion annosum* (Fr.) Bref. (white, stringy rot) or *Verticicladiella* spp. (resin-soaked, dark stain) were absent. Tissue samples from the roots were plated on 2% malt extract agar and media selective for *Fusarium* (Agrawal et al. 1973) and *Heterobasidion annosum* (Kuhlman and Hendrix 1962). An array of saprophytic fungi were isolated on all media. The root system of a fourth declining Virginia pine appeared to be normal and showed little evidence of decay.

The Virginia pines at the Champion International seed orchard are grafted on loblolly (*P. taeda* L.) root stock. Although the root decay observed at the Hammermill orchard was not observed at the Champion Orchard, resin-soaked lesions on the main roots were readily apparent. Root tissue isolation from these lesions yielded *F. oxsporum* Schlecht. (53%), *F. moniliforme* var. *subglutinans* (35%), and *F. solani* (Mort.) Sacc. (12%) on the *Fusarium*-selective media; but on *Heterobasidion annosum* - selective media and 2% malt extract agar, only saprophytes were recovered.

In both seed orchards, chainsaw sections through the bole at several heights revealed extensive blue stain. Since the sudden decline of these trees was similar to symptoms of pine wilt (Dropkin et al. 1981; Wingfield et al. 1982), and the pinewood nematode was first found in association with blue-stain in longleaf pine (P. palustris Mill.) (Steiner and Buhrer 1934), bole samples were brought to the laboratory and assayed for the pinewood nematode. Large numbers of nematodes were extracted from these samples using a pie pan technique (Cairns 1960). The nematodes matched the description of Bursaphelenchus xylophilus (Steiner & Buhrer 1934; Nickle et al. 1981). Although B. xylophilus often colonize in all parts of infested pine trees (Dropkin et al. 1981), none were recovered from root systems of the grafted Virginia pines we excavated. We found only saprophytic nematodes in deteriorated root systems of the trees we excavated.

In January 1983, two rapidly declining Virginia pines were observed in a progeny test at the Baldwin State Forest near Milledgeville, Ga. Tissue samples from bole sections cut at 18 inch intervals with a chainsaw from these trees yielded as many as 852 pinewood nematodes/g sapwood fresh wt ($\bar{x} = 352$). This was the first report of the pinewood nematode in Georgia (Dwinell and Barrows-Broaddus 1983).

To determine the pathogenicity of the Alabama population of B. xylophilus, we inoculated 2-year-old seedlings of Virginia and loblolly pines grown in plastic flats (33 x 13 x 11 cm) which contained a mixture of soil, pine bark, and sand (2:1:1 v:v:v). Near the top of each stem, the bark was removed, and a moistened plug of cotton infested with 5,000 nematodes from a population increased on cultures of Botrytis cinerea (Dropkin et al. 1981) was attached with foil.

Each of four flats contained 12 seedlings. Four loblolly seedlings had been inadvertently planted among these four trays of Virginia pines and were not able to compete satisfactorily. Within 1 month these four seedlings began to decline. With the onset of mortality, serial sections cut from the seedlings were placed in 10 ml of sterile water in test tubes for 48 hrs. The number of nematodes extracted averaged 16 per cm of stem tissue. The greatest concentration of nematodes was near the base of the seedlings (120 nematodes/cm). In contrast, only 2 of 20 Virginia pines died. The Virginia pines, however, were more vigorous than the loblolly pines at the time of inoculation. A better test of pathogenicity of pinewood nematode might have been accomplished on stressed Virginia pine seedlings.

Biotic and abiotic factors that stress conifers apparently predispose them to infection by the pinewood nematode (Dropkin et al. 1981; Adams Wingfield et al. 1982). The 1981 drought in South Carolina probably contributed to the increased susceptibility of Virginia pines at the Champion International seed orchard. In Alabama at the Hammermill orchard, root pruning produced by subsoiling in the summer of 1982 wounded root systems and increased moisture stress in these trees, probably contributing to the deterioration of the root systems and infestation of the trees by B. xylophilus. Cultural activities that wound roots increase the risk of root disease development (Horner and Alexander 1983). Pitch canker in seed orchards may also contribute both directly and indirectly to the pine wilt problem. On main stems, these cankers adversely affect translocation, which probably increases susceptibility to infection by B. xylophilus. Also since this nematode is mycophagous (Dropkin et al. 1981), it it might feed on the pitch canker fungus, F. moniliforme var. subglutinans.

Whether or not the pinewood nematode is a primary pathogen in seed orchards is open to question. As Wingfield (1983) recently noted, the nematode may be transmitted to dead and dying trees without necessarily being the primary cause or their death. In a study on jack pine (Pinus banksiana Lamb.) infected with dwarf mistletoe, Burnes et al. (1983) found that cerambycid beetles and B. xylophilus were secondary colonizers of declining trees.

The decline of Virginia pines in seed orchards is a complex problem because of the number of biotic and abiotic factors involved. Research is needed to elucidate the role of the pinewood nematode in declining pines in seed orchards in the South.

PITCH CANKER

F. moniliforme var. subglutinans, like many canker-producing organisms, requires a wound as an infection court. Routine seed orchard management practices such as branch pruning, mowing, and cone removal create wounds for the entry of the pathogen. Weather-related injuries caused by wind, ice, and hail may also serve as entry points. Kelley and Williams (1982) suggested that wounds on loblolly pines caused by Hurricane Frederic in September 1979 provided infection courts for the pitch canker fungus, resulting in an epidemic in one loblolly pine seed orchard in Alabama. A tornado probably caused intensification of pitch canker in another Virginia pine seed orchard managed by Kimberly-Clark at Coosa Pines, Al. (Dwinell and Barrows-Broaddus 1981). The development of cankers in branch crotches of Virginia pines at the Hammermill seed orchard probably resulted from heavy ice accumulation on the trees during an ice storm in 1982.

In July 1981 we established a study in a Virginia pine progeny test at Coosa Pines, Al. to determine if isolates of the pitch canker pathogen varied in their ability to invade Virginia pines. Two isolates each of F. moniliforme var. subglutinans recovered from cankers on Virginia (D-25; D-26) and shortleaf (P. echinata Mill.) (D-29; D-30) pines were used to inoculate 20 11-year-old Virginia pines. The trees were wounded with a hammer and chisel by removing a 3 cm^2 area of bark at 1.3 m above ground to expose the cambium. Ten replicate wounds (2 per tree) were sprayed to run-off with 10^6 conidia/ml suspensions of each isolate. Five trees served as wounded, but uninoculated controls. After 14 months, treated sections of the boles from each of the 25 trees were brought to the laboratory for analysis. The outer bark was removed and the length, width, and area of each canker were measured. At the point of the original wound, each bole section was cut in cross-section with a bandsaw to permit the measurement of the extent of resin-soaking of the sapwood. Tissue samples from the edges of the cankers were plated on a Fusarium-selective medium (Agrawal et al. 1973).

All trees inoculated with the pitch canker fungus exhibited main stem cankers after 14 months. Although cankers caused by isolate D-26 from Virginia pine were generally smaller than those caused by other isolates, differences in canker size among isolates were not statistically significant (Table 1). Over all treatments, canker length averaged 32.2 cm and width averaged 7.8 cm. The area of resin-soaked wood (11.4 cm^2) represents about 11% of the area of the bole. The pitch canker fungus was reisolated from 65% of the cankers. Isolations from control trees showed little evidence of natural infection by the pitch canker fungus. Wounds on these trees showed signs of healing after 14 months. The time of the year (July) that wounds were made on control trees may have accounted for this lack of natural infection. In a study on the epidemiology of pitch canker in a loblolly pine seed orchard, Kuhlman et al. (1982) found that fall and winter inoculations were more successful than those in spring and summer. Inoculation of wounds on slash pine with the pitch canker fungus in September was more favorable to the growth of the pathogen than were inoculations in June (Barrows-Broaddus 1983).

Table 1. Dimensions of pitch canker on Virginia pines in a progeny test area 14 months after inoculation with four isolates of F. moniliforme var. subglutinans

Isolates		Canker size[a]			Area of resin-soaked wood[b]
No.	Pine host	Length (cm)	Width (cm)	Area (cm^2)	(cm^2)
D-25	Virginia	37.2	8.9	296.9	13.4
D-26	Virginia	25.2	5.9	133.2	5.4
D-29	Shortleaf	30.7	8.1	222.2	14.4
D-30	Shortleaf	35.6	8.1	257.4	12.5
Mean[c]		32.2*	7.8*	227.4*	11.4*
Control		4.3	1.8	7.3	0

[a] Data based on five trees/isolate

[b] Cross-sectional area through the point of wounding

[c] * Denotes means for treatments are significantly different from control means ($P \geqslant 0.01$)

Since circumstantial evidence from a previous study (Dwinell and Barrows-Broaddus 1981) indicated that the pitch cankers on slash pine could be initiated by infection through branch stubs, fresh branch stubs were created with clippers and sprayed with a spore suspension of an isolate (D-25) of F. moniliforme var. subglutinans on five additional Virginia pine trees in the Coosa Pines area. All 10 of the branch stubs (2 per tree) that had been inoculated became infected and were resin soaked. In 4 stubs, the pathogen grew into the bole from the stub, causing a resinous canker to develop on the main stem adjacent to the inoculated branch stub.

DISEASE CONTROL

The lack of information on various aspects of the disease cycle of both pitch canker and pine wilt has delayed the development of suitable control measures in Virginia pine seed orchards. Since wounds are a prerequisite for the initiation of pitch canker, we suggest that management practices be modified to reduce the wounding of trees. The practice of root pruning to increase seed production should be re-evaluated because the damage causes stress on trees and predisposes them to attack by longhorn beetles and subsequent infestation by the pinewood nematode. Root pruning also increases the risk of root disease caused by pathogenic fungi.

Disease control in seed orchards should also include: (1) establishment of orchards on suitable sites, (2) adjusting fertilizer schedules to avoid over-fertilization, and (3) controlling insect vectors (Blakeslee et al. 1980). For example, Fraedrich and Witcher (1982), stated that excess nitrogen increased pitch canker severity on loblolly, slash, and Virginia pines. Barnett and Thor (1978) found that Virginia pine trees growing on poorly drained sites were more susceptable to pitch canker than those on well drained sites.

Since individual clones within species vary greatly in their susceptibility to infection by F. moniliforme var. subglutinans (Dwinell et al. 1977; Dwinell and Barrows-Broaddus 1981; Kelley and Williams 1982; Kuhlman et al. 1982), it may be possible to select for resistance to pitch canker disease. Barnett and Thor (1978) suggested that resistance to pitch canker was controlled by either dominance or epistatic gene action. Barrows-Broaddus (1983) observed in a greenhouse study on Virginia pine that, when seedlings were inoculated with F. moniliforme var. subglutinans, certain pine progeny exhibited partial resistance to disease development.

Seed orchard establishment and maintenance are expensive. The threat of serious losses from pine wilt and pitch canker diseases requires that we develop means to successfully control these two diseases to avoid considerable economic losses in the future.

LITERATURE CITED

Agrawal, S. C., M. N. Khare, and L. S. Kushwara. 1973. A selective medium for isolation and quantitative estimation of Fusarium in soil. Sci. Culture 39:555-556.

Anonymous. 1982. 1981 Directory of forest tree seed orchards in the United States. USDA For. Serv., FS-278. 48 p.

Barrows-Broaddus, J. 1983. Pitch canker of southern pines: histopathology and biocontrol of the causal agent Fusarium moniliforme var. subglutinans, Ph.D. Dissertation, North Carolina State University, Raleigh. 120 p.

Barrows-Broaddus, J. and Dwinell, L. D. 1979. Variation in virulence of diverse sources of Fusarium moniliforme var. subglutinans on Virginia and loblolly pine. Phytopathology 69:525. (Abstr.)

Barnett, P. E. and E. Thor. 1978. Effects of site and inheritance on Fusarium incidence in Virginia pine. Proc. Symp. for the management of pines of the interior South. USDA For. Serv. State and Private For. Tech. SA-TP2. Atlanta. p. 159-161.

Blakeslee, G. M., L. D. Dwinell and R. L. Anderson. 1980. Pitch canker of southern pines; identification and management considerations. USDA For. Serv. Southeast. Area State and Private For. For. Rep. SA-FR11. Atlanta. 15 p.

Box, B. H. and R. R. Foil. 1978. Managing Virginia pines for Christmas-tree production in Louisiana. Agric. Exp. Stn. Res. Release. Louisiana State University. Note 76. 2 p.

Burnes, T. A., M. J. Wingfield, F. A. Baker and D. W. French. 1983. The pine wood nematode in dwarf misltetoe infested jack pine in Manitoba. Phytopathology 73:834 (Abstr).

Cairns, J. 1960. Methods in nematology: a review. pp 33-84. In Sasser, J. N. and W. R. Jenkins (eds). Nematology. Fundamental and recent advances with emphasis on plant parasitic and soil forms. The University of North Carolina Press, Chapel Hill. 480 pp.

Chandler, J. W. 1979. Growing Christmas trees in Texas. Texas Agricultural Extension Service. The Texas A&M University System, College Station. No. 1733. 3 pp.

Dropkin, V. A., A. Foudin, E. Kondo, M. Linit and M. Smith. 1981. Pinewood nematode: a threat to U.S. forests? Plant Dis. 65:1022-1027.

Dwinell, L. D. 1978. Susceptibility of southern pines to infection by Fusarium moniliforme var. subglutinans. Plant Dis. Rep. 62:108-111.

Dwinell, L. D. and J. Barrows-Broaddus. 1981. Pitch canker in seed orchards. In Proc. 16th South. Forest Tree Improv. Conf. p. 234-240 (Blacksburg, Va., May 1981).

Dwinell, L. D. and J. Barrows-Broaddus. 1983. Pine wilt of Virginia pine in seed orchards. Phytopathology 73:834 (Abstr).

Dwinell, L. D., P. L. Ryan and E. G. Kuhlman. 1977. Pitch canker of loblolly pine in seed orchards. In Proc. 14th South. For. Tree. Improv. Conf. p. 130-137. (Gainesville, Fla., June 1977).

Fraedrich, B. R. and W. Witcher. 1982. Influence of fertilization on pitch canker development on three southern pine species. Plant Dis. 66:938-940.

Gibson, I. A. S. and T. Jones, 1976. Monocultures as the origin of major forest pests and diseases. 18th Br. Ecol. Soc. Symp., Oxford, 1976 p. 139-161.

Hepting, G. H. 1954. Gum flow and pitch-soak in Virginia pine following Fusarium inoculation. Southeast. For. Exp. Stn., Paper 40. Asheville, N.C. 10p.

Hepting, G. A. and E. R. Roth. 1946. Pitch canker, a new disease of southern pines. J. For. 44:742-744.

Horner, W. E. and S. A. Alexander. 1983. *Verticicladiella procera* in pine seed orchards in the South. Phytopathology 73:835 (Abstr).

Kelly, W. D. and J. C. Williams. 1982. Incidence of pitch canker among clones of loblolly pine in seed orchards. Plant Dis. 66:1171-1173.

Kuhlman, E. G. and F. F. Hendrix, Jr. 1962. A selective medium for the isolation of *Fomes annosus*. Phytopathology 52:1310-1311.

Kuhlman, E. G., L. D. Dwinell, P. E. Nelson and C. Booth. 1978. Characterization of the *Fusarium* causing pitch canker of southern pines. Mycologia 70:1131-1143.

Kuhlman, E. G., S. D. Dianis, and T. K. Smith. 1982. Epidemiology of pitch canker disease in a loblolly pine seed orchard. Phytopathology 72:1212-1216.

Murray, B. R., J. W. Demski, T. S. Davis and D. C. Bachtel. 1981. Christmas tree production in the state of Georgia. Amer. Christmas Tree Journal. pp. 21-24.

Nickle, W. F., A. M. Godden, Y. Mamiya, and W. P. Wergin. 1981. On the taxonomy and morphology of the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer 1934) Nickle 1970. J. Nematology 13:385-392.

Shea, K. R. 1971. Disease and insect activity in relation to intensive culture of forests. p. 109-118. *In* Proc. of the 15th International Union of Forest Research Organizations, Sec. t. 32.

Steiner, G. and E. M. Buhrer. 1934. *Aphelenchoides xylophilus*, n. sp., a nematode associate with blue-stain and other fungi in timber. J. Agr. Res. 48:919-951.

Utz, F. A. and W. E. Balmer. 1980. Growing Christmas trees in the South. USDA For. Serv., Southeast. Area, State and Private For., General Report SA-GR 5. Atlanta. 26 p.

Williston, H. L. and W. E. Balmer. 1980. Management of Virginia pine. USDA For. Serv., Southeast. Area, State and Private For., FR-SA-FB 7. Atlanta. 5 p.

Wingfield, M. J., R. A. Blanchette, T. H. Nicholls and K. Robbins. 1982. Association of pine wood nematode with stressed trees in Minnesota, Iowa and Wisconsin. Plant Dis. 66:934-947.

Wingfield, M. J. 1983. Transmission of pine wood nematode to cut timber and girdled trees. Plant Dis. 67:35-37.

CYTEX® AND OTHER CHEMICALS EFFECTIVELY INHIBIT CONELET ABORTION IN LONGLEAF PINE

Robert C. Hare[1]

Abstract.--Yields in longleaf pine seed orchards could be much improved by treating foliage and conelets in spring with anti-abortion chemicals. Cytex®, an extract of marine algae, is an economical source of cytokinin activity. When applied operationally as a 1 percent foliar spray using a mist blower, Cytex increased first-year conelet retention from 33 to 62 percent, 51 to 78 percent, and (with boron) from 33 to 72 percent respectively in three separate annual tests. The anti-abscission chemicals 8-hydroxyquinoline, cobalt chloride, and picloram increased first-year cone retention from 51 percent to 83, 81, and 75 percent, respectively, in 1982.

Premature shedding of conelets (1st year female strobili) is a serious problem in longleaf pine (Pinus palustris Mill.) tree improvement programs. In some years 90 percent or more of the conelets are shed prematurely (White et al. 1977), leading to the typically low seed yields in most longleaf pine orchards (Hare 1981). The cause of this "physiological drop" of conelets, which is not due to cone insects or lack of pollination, is unknown but may be related to ethylene production by the foliage or expanding shoots. Foliar sprays with antiethylene compounds or cytokinins have been shown to decrease conelet loss by half and increase seed yield per original conelet up to six-fold (Hare 1981). Boric acid (B) added to the sprays enhanced the effects of some active compounds.

Although several compounds were shown to be effective, none of the antiethylene compounds are available commercially, and purified cytokinins like benzyladenine (BA) are very expensive. A more economical commercial product with cytokinin activity is Cytex®[2] (Atlantic and Pacific Research, Inc., North Palm Beach, Florida). Cytex (CX) is an aqueous extract of marine algae with about 100 ppm kinetin equivalents by bioassay (Brain et al. 1973, Ketring and Schubert 1981). Three bioassay methods were used, based on fresh weight increases in carrot explants, radish leaf discs, and callus cultures. It is registered for increasing yield by stimulating growth in a number of agricultural crops (tomato, potato, celery, citrus). In a preliminary 1980 experiment, the effects of 0.1 percent BA and 1, 3, and 5 percent CX on conelet abortion were compared in a longleaf pine seed orchard. Conelet-bearing branches on three trees each were sprayed in late April with water, BA, or CX, all containing 0.1 percent Tween-20 surfactant. Conelet survival in October averaged 28 percent for water control, 38 percent for BA, and 53 percent for the 1 percent CX. Higher levels of CX were less effective. CX thus appears to be a practical substitute for BA.

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[2] The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U. S. Department of Agriculture of any product or service to the exclusion of others which may be suitable.

In addition to the six chemicals already reported (Hare 1981), there are a number of chemicals with reported anti-abscission, antiethylene, or cytokinin activity which might be investigated. Aminooxyacetic acid (AOA) inhibited ethylene synthesis in carnation (Broun and Mayak 1981), Tordon (TORD) (picloram) inhibited citrus abscission (Einset et al. 1981), coumarin (COUM) inhibited coleus leaf abscission (Gupta 1970), cobalt ($CoCl_2$) inhibited ethylene synthesis in bean and apple (Lau and Yang 1976), 8-hydroxyquinoline (8-HQ) is a powerful ethylene synthesis inhibitor (Parups and Peterson 1973), and 3,5-diiodo-4-hydroxybenzoic acid (DIHB) inhibits ethylene production by cress roots (Robert et al. 1975). Purines related to BA which might have cytokinin activity include dodecylaminopurine (DDAP) and 6-chloropurine (6-CP), both obtained from Polaroid Corporation.

This study investigates the effects of CX and the above chemicals on conelet abortion in longleaf pine seed orchards. Experiment 1 was a pilot study to see if CX could be used operationally with a mist blower to increase seed yield. Two levels of CX were tested with and without two levels of B, all compared to a surfactant control. Experiment 2 was an exploratory study to compare the effectiveness of nine chemicals and a control using a hand sprayer and bucket truck.

MATERIALS AND METHODS

Experiment 1.--Ninety 19-year-old grafted longleaf pine trees at the Erambert Seed Orchard in south Mississippi were selected on the basis of good seed cone production, ignoring clones. In April 1982, healthy first year conelets were counted on each tree, and 10 trees at random were assigned to each of nine treatments (Table 1). All solutions contained 0.05 percent (v/v) Aromox C/12W® surfactant (Armak Corp., McCook, Ill.). Solutions were applied on May 4, using a mist blower and thoroughly wetting the crown from opposite sides of each tree. Surviving conelets were counted in October 1982.

Experiment 2.--In April 1982, 50 trees with good seed cone production were selected in the orchard, first-year conelets were counted, and five trees were assigned at random to each of 10 treatments (Table 1). In early May, treatments were applied by spraying conelet-bearing branches to the point of runoff with the appropriate solution from a hand pressure sprayer, using a bucket truck. All solutions contained 0.05 percent Aromox C/12W. Surviving cones were counted in October.

For both experiments, the percentage of spring conelets per tree surviving in October was used as the basis for analyses of variance and Duncan's multiple range test.

Table 1.--Chemicals and concentrations used in two foliar spray experiments[1]

Experiment 1			Experiment 2	
Treatment[2]	Chemical Concent. CX	B[2]	Treatment[2]	Chemical Concent.
	%			mg/1
Ck	0	0	Ck	control
CX-1	1	0	AOA	10.0
CX-2	2	0	TORD	0.6
B-1	0	0.13	BA	1000.0
B-2	0	0.26	DDAP	1000.0
CX-1 + B-1	1	0.13	6-CP	1000.0
CX-1 + B-2	1	0.26	COUM	100.0
CX-2 + B-1	2	0.13	$CoCl_2$	1000.0
CX-2 + B-2	2	0.26	8-HO	100.0
			DIHB	200.0

[1] All solutions contained 0.05 percent Aromox C/12W®

[2] CX = Cytex, B = boric acid, AOA = Aminooxyacetic acid, TORD = Tordon (picloram), BA = benzyladenine, DDAP = dodecylaminopurine, 6-CP = 6-chloropurine, COUM = coumarin, 8-HQ = 8-hydroxyquinoline, and DIHB = 3,5-diiodo-4-hydroxybenzoic acid.

RESULTS AND DISCUSSION

Experiment 1.--The best conelet retention occurred using 1 percent CX, with 78 percent survival compared to 51 percent in the control (Fig. 1). The 2 percent CX spray was not significantly better than the control. In the 1980 experiment summarized in Table 2, 1 percent CX was also better than 3 or 5 percent, suggesting that CX may be inhibitory above 1 percent. Boric acid had no significant effect here, but its effects have been inconsistent (Table 2). Conelet retention was excellent with B alone in 1978 but the same concentration in 1979 was ineffective (Hare 1981). The inconsistencies may be related to variabilities in soil B content. The CX experiments summarized in Table 2 indicate that applying a 1 percent CX solution with the mist blower is an effective and economical way to improve longleaf pine orchard seed yields. Addition of 0.3 percent B may help.

The years 1981 and 1982 were exceptionally good conelet retention years in southern Mississippi, with over 50 percent retention from May to October (Table 2). In the previous 3 years controls ranged from 12 to 33 percent retention. High conelet retention levels in control trees reduce treatment effects on a percentage basis.

Experiment 2.--All but three of the nine compounds significantly increased conelet survival (Fig. 2). The best treatments were 8-hydroxyquinoline (83 percent survival), $CoCl_2$ (81%), and picloram (Tordon) (75%). Coumarin, 6-CP, DIHB, and BA treatments showed about 70 percent survival, compared to 51 percent for the control. Eight-hydroxyquinoline is a strong ethylene synthetis inhibitor used to preserve cut flowers (Larsen and Frolich 1969). It is available commercially, as are $CoCl_2$, Tordon, and coumarin. These compounds and H_3BO_3 in combination with CX will be compared in 1983.

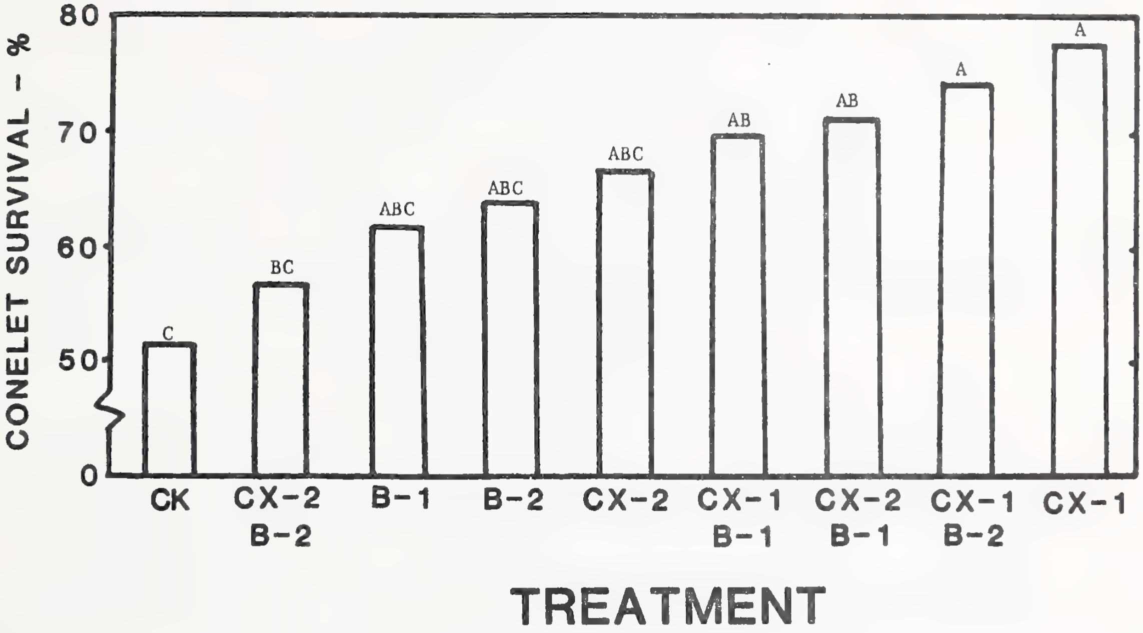

Figure 1.--Percent average survival of conelets in Experiment 1 by treatment, May to October. Bars with same letter do not differ significantly, $P = 0.05$. CK = control, CX-1 = 1 percent Cytex®, CX-2 = 2 percent Cytex®, B-1 = 0.13 percent boric acid, B-2 = 0.26 percent boric acid.

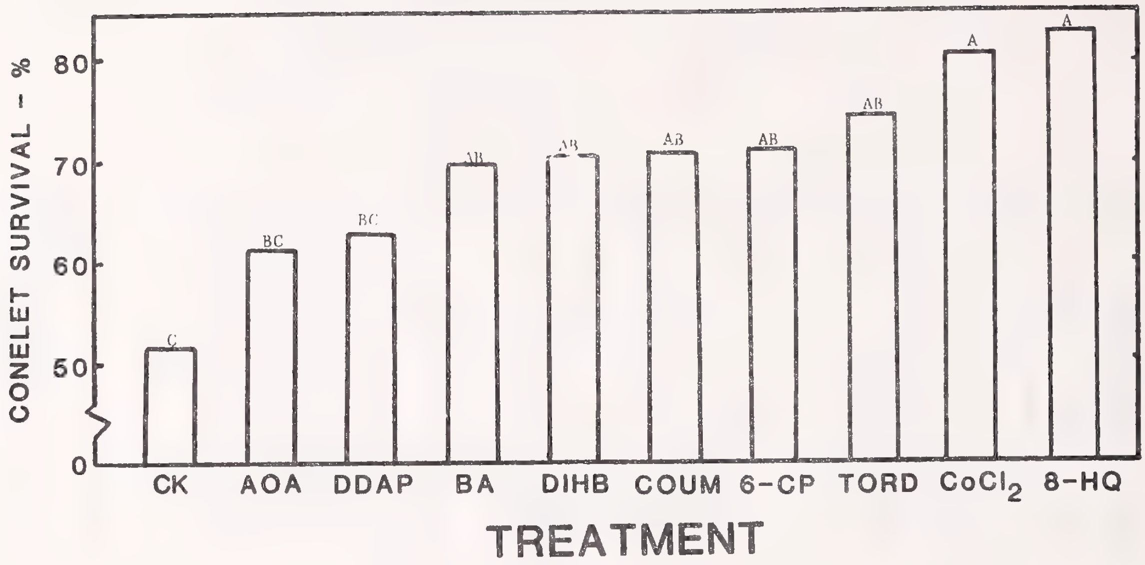

Figure 2.--Percent average survival of conelets by treatment in Experiment 2, May to October. Bars with same letter do not differ significantly, P = 0.05. See Table 1 for chemical abbreviations and concentrations.

Table 2.--Summary of six longleaf pine conelet abortion experiments, using boric acid and a cytokinin source.

		Chemicals used as foliar sprays[1]								
Exp. Year	Type of Application	Control	B	PBA or BA	1% CX	2% CX	3% CX	5% CX	BA + B	CX 1% + B
		Percent[2]								
1978	Hand sprayer	19	49	55	--	--	--	--	--	--
1979	Hand sprayer	15	16	35	--	--	--	--	52	--
1980	Mist blower	12	32	25	--	--	--	--	21	--
1980	Hand sprayer	33	--	42	62	--	18	34	--	--
1981	Mist blower	53	64	--	57	--	--	--	--	72
1982	Mist blower	51	64	--	78	66	--	--	--	74

[1] PBA = (N-benzyl-9-(tetrahydro-2H-pyran-2yl)-adenine, BA = benzyladenine, B= boric acid, CX = Cytex®

[2] Percent of May conelets surviving in October of the treatment year.

LITERATURE CITED

Brain, K. R., M. C. Chalopin, T. D. Turner, G. Blunden, and P. B. Wildgoose. 1973. Cytokinin activity of commercial aqueous seaweed extract. Plant Sci. Ltrs. 1:241-245.

Broun, R., and S. Mayak. 1981. Aminooxyacetic acid as an inhibitor of ethylene synthesis and senescence in carnation flowers. Sci. Hortic. 15: 277-282.

Einset, J. W., J. L. Lyon, and D. L. Sipes. 1981. Citrus tissue culture. Auxins in relation to abscission in excised pistils. Plant Physiol. 67:1109-1112.

Gupta, S. K. 1970. Inhibitory effect of coumarin on abscission of Coleus blumei Benth. explant petioles. Ind. J. Exp. Biol. 70:155-156.

Hare, R. C. 1981. Reducing conelet abortion in longleaf pine with chemicals. Can. J. For. Res. 11:448-450.

Ketring, D. L., and A. M. Schubert. 1981. Reproduction of peanuts treated with a cytokinin-containing preparation. Agron. J. 73:350-352.

Larsen, F., and M. Frolich. 1969. The influence of 8-hydroxyquinoline citrate, B-Nine and sucrose on respiration and water flow in "Red Sim" cut carnations in relation to flower senescence. J. Amer. Soc. Hort. Sci. 94:289-292.

Lau, O. L., and S. F. Yang. 1976. Inhibition of ethylene production by cobaltous ion. Plant Physiol. 58:114-117.

Parups, E. V., and E. A. Peterson. 1973. Inhibition of ethylene production in plant tissues by 8-hydroxyquinoline. Can. J. Plant Sci. 53:351-353.

Robert, M. L., H. F. Taylor, and R. L. Wain. 1975. Ethylene production by cress root segments and its inhibition by 3,5-diiodo-4-hydroxybenzoic acid. Planta 126:273-284.

White, T. L., H. H. Harris, Jr., and R. C. Kellison. 1977. Conelet abortion in longleaf pine. Can. J. For. Res. 7:378-382.

MEASURING POLLEN CONTAMINATION IN CLONAL SEED ORCHARDS WITH THE AID OF GENETIC MARKERS

D. B. Smith and W. T. Adams[1]

Abstract.--The availability of electrophoretic techniques has provided a large number of simply inherited genetic markers (allozymes) which can be used to estimate levels of pollen contamination in seed orchards. Using several allozyme loci, the multilocus genotypes of both the male and female gametes contributing to a conifer embryo can be determined. Because natural stands contain many more adult genotypes than do clonal orchards, they are expected to produce a much greater variety of multilocus pollen genotypes, even when there are no differences in single locus allele frequencies between orchards and background stands. The level of pollen contamination in an orchard can be estimated by analyzing a sample of orchard seed and determining the proportion of pollen gametes having multilocus genotypes which could not be produced in the orchard. This proportion is then divided by the probability that a background pollen grain has a multilocus marker (i.e., a genotype different from those that can be produced by orchard clones) to compute the level of contamination. Estimates of pollen contamination in several blocks of a Douglas-fir seed orchard in western Oregon are used to illustrate this multilocus technique. Preliminary recommendations for its use are also discussed.

Additional keywords: allozymes, migration models, pollen management, *Pseudotsuga menziesii*.

In order to avoid pollen contamination from non-orchard (background) sources, seed orchards should be located far from stands of the same species. In most circumstances, however, this is not practical and pollen dilution zones are often employed in an attempt to keep levels of pollen contamination low. Although few direct estimates of pollen contamination have been made, it appears that pollen dilution zones may not be as effective as intended and that pollen contamination can be a serious problem in seed orchards (Squillace 1967, Squillace and Long 1981, Friedman and Adams 1981). In addition to pollen dilution zones, other management techniques for minimizing pollen contamination have been suggested, but their effectiveness is largely unknown (Silen and Keane 1969, Denison and Franklin 1975, Bridgwater and Trew 1981).

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Recommendations for seed orchard location and pollen management (e.g., size of dilution zones) have generally been based on measures of pollen dispersion and differences between orchards and background stands in floral phenology (Wang et al. 1960, Schmidt and Hamblett 1962, Silen 1962, 1963). Such measures give some indication of the relative proportions of orchard and non-orchard pollen present in an orchard at the time of pollination, but do not provide estimates of their relative effectiveness in fertilization. The availability of techniques for directly estimating pollen contamination would enable seed orchard managers to determine the need for and success of pollen management efforts.

Direct estimates of pollen contamination can be made with the aid of genetic markers and the following well known migration model:

$$Q_o = \bar{q}_b m + q_o(1-m) \qquad (1)$$

where

Q_o = frequency of a marker in pollen gametes which have fertilized orchard ovules,

$\bar{q}_b$ = mean frequency of the same marker in pollen produced by background stands,

q_o = frequency of the marker in orchard pollen,

m = proportion of orchard ovules fertilized by pollen from background stands, and

1-m = proportion of orchard ovules fertilized by orchard pollen (Spiess 1977).

The rate of pollen contamination (m) is estimated by solving (1) for m and substituting estimates of marker frequencies so that:

$$\hat{m} = \frac{\hat{Q}_o - \hat{q}_o}{\hat{\bar{q}}_b - \hat{q}_o} \qquad (2)$$

Particularly useful are markers unique to background pollen sources such that (2) reduces to:

$$\hat{m} = \hat{Q}_o / \hat{\bar{q}}_b \qquad (3)$$

Estimates of pollen contamination using genetic markers have recently been reported for slash pine (Squillace and Long 1981) and loblolly pine (Friedman and Adams 1981).

In the past, application of this method has been limited by the lack of suitable genetic markers; but with the advent of electrophoresis in recent years, a large number of simply inherited genetic markers (allozymes) have become available. There are many advantages of using allozymes as genetic markers for tree improvement research problems (Adams 1982). Advantages of particular relevance to pollen contamination studies include: (1) the ability (in conifers) to identify the genotypes of the male and female gametes contributing to an embryo, and (2) the high levels of variation at allozyme loci.

Pollen contamination estimates based on single locus genetic markers require at least moderate gene frequency differences between an orchard and the background stand; otherwise, the efficiency of estimates is low, and very large sample sizes are required to achieve a reasonable level of precision. Unfortunately, the majority of allozyme variation that has been observed in forest tree species seems to occur within populations. Gene frequency differences among populations, even those separated by large distances, are often quite small (Brown and Moran 1979, Adams 1982). The same lack of differentiation appears to be true when allozyme frequencies in seed orchards and background stands are compared. For example, gene frequencies among clones (25 to 27) in three of ten 5 acre (2.0 ha) blocks in the Beaver Creek Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seed orchard (USDA Forest Service, Siuslaw National Forest, Oregon) and among adult trees in the surrounding natural stand are compared for three allozyme loci in Table 1. Each orchard block represents a different breeding zone (geographical region), all of which are different from the zone within which the orchard is located. Although large differences among blocks, and between blocks and the background stand, might be expected, only limited gene frequency differences and the presence or absence of alleles in low frequency were found.

Table 1.--Allele frequencies at three allozyme loci in three blocks of the Beaver Creek Douglas-fir seed orchard and in the surrounding (background) natural stand.[a]

		Orchard block			
Locus	Allele	7	5	10	Background
GOT3	1	.027	.142	.217	.078
	2	.970	.858	.749	.904
	3	.003	--	.034	.018
LAP1	2	.361	.614	.449	.482
	5	.236	.238	.296	.255
	7	.403	.148	.255	.263
IDH	1	.084	.113	.149	.168
	2	.872	.814	.820	.743
	3	.041	.026	--	.080
	4	.003	.047	.031	.009

[a] Allele frequencies are based on the genotypes of all 25 to 27 clones in each of the three orchard blocks and on a sample of 183 (LAP1, IDH) or 57 (GOT3) trees in the background stand.

While limited gene frequency differences between orchards and background stands may preclude the use of single locus allozyme markers for estimating pollen contamination, a technique based on combining allozyme data over multiple loci shows a great deal of promise. In this paper, we introduce and illustrate this multilocus technique which can be used in clonal seed orchards even in the absence of gene frequency differences between orchards and background stands.

DESCRIPTION OF THE MULTILOCUS TECHNIQUE

The multilocus estimation technique takes advantage of the large amount of allozyme variation observed among trees within populations. It is based on the premise that a limited number of multilocus genotypes exist among the clones in any one orchard, relative to the number in background stands. Thus, even when there are no differences in allele frequencies between an orchard and a background stand, the background stand can be expected to produce a greater variety of multilocus pollen genotypes than the orchard. Furthermore, as the number of variable loci included in an analysis increases, the ability to distinguish pollen gametes produced in the background stand from those produced in the orchard will also increase. The expected proportion of orchard ovules fertilized by background pollen with multilocus markers (i.e., multilocus genotypes that are unique to the background stand) is:

$$b = md \tag{4}$$

where

m = probability that an orchard ovule is fertilized by a pollen grain from the background stand, and

d = probability that a background stand pollen grain has a multilocus marker.

The rate of pollen contamination is then estimated as:

$$\hat{m} = \hat{b}/\hat{d}. \tag{5}$$

Application of this multilocus pollen contamination estimator ($\hat{m}$) requires that the allozyme genotypes of all clones in an orchard be determined for each locus used in the analysis. In conifers, clone genotypes can be inferred from the allelic composition of megagametophytes in a sample of seeds, or determined directly by analyzing bud or needle tissues (Adams 1982). The multilocus genotypes of the clones are then used to generate the array of all multilocus pollen genotypes which can be produced by the orchard. For example, using 14 variable allozyme loci, the number of multilocus pollen genotypes that can be produced by the clones in each Beaver Creek block ranges from 154 to 416. In contrast, the number of multilocus gametic combinations that are possible with the alleles in each block is over a million. Therefore, it is not unreasonable to expect the natural stand surrounding this orchard (with much larger numbers of adult genotypes) to produce many pollen gametes with multilocus genotypes which could not be produced in the orchard blocks.

Once allozyme genotypes of the orchard clones are known, embryos from a sample of orchard seed are analyzed and the genotypes of pollen gametes inferred. The multilocus genotype of each pollen gamete in the seed sample is compared to the array of pollen genotypes which can be produced by the orchard clones. The observed proportion of pollen gametes with genotypes not matching those from the orchard clones (i.e., observed contaminants) is $\hat{b}$. The probability of observing contaminants (if they are present) will increase as the number of variable loci used in the analysis increases.

To estimate d, genotypes of a representative sample of adult trees in the background stand must be determined. From these adult genotypes it is possible to infer the frequencies of multilocus pollen gametes produced in the background stand. The frequency of pollen gametes with multilocus markers ($\hat{d}$) can then be calculated as one minus the total frequency of indistinguishable pollen gametes. Indistinguishable pollen gametes are those gametes which can be produced in both the orchard and the background stand.

Estimated frequencies of the indistinguishable pollen gametes in the background stand can be inferred from the adult genotypes in one of two ways. In the first, all possible allelic combinations of loci used in the analysis are generated for each sample tree. Since information on linkage relationships (i.e., whether linked genes are in "coupling" or "repulsion") is generally not available, we make the simplifying assumption that all gametic types from each sample tree are produced in equal frequency. The estimated frequency of each indistinguishable pollen gamete in the background stand is then calculated as its unweighted mean frequency among gametes of all sample trees. The second method of estimating the frequencies of indistinguishable pollen gametes utilizes single locus allele frequencies which are computed from the sample of adult genotypes. The frequency of each indistinguishable pollen gamete in the background stand is assumed to be the product of its component allele frequencies. This method is somewhat simpler computationally than the first, since all possible multilocus gametic combinations do not have to be generated for each sample tree. In practice, we have found that both methods lead to very similar estimates of d, and for the examples in the next section the second method was employed.

Both of the above methods for estimating multilocus pollen frequencies assume that: (1) the genes used in the analysis are in linkage equilibrium in the background stand, and (2) pollen productivity is independent of multilocus gametic genotype. In large outcrossing populations of forest trees, the first assumption is probably not violated to any great degree, and if it were, it is not clear what effect, if any, this would have on estimates of m. The second assumption seems to be reasonable, especially when a large number of variable loci are utilized, because each multilocus gamete can be produced by a variety of adult genotypes. Certainly, genetic markers based on alleles at one or a few loci would be much more sensitive to violations of the second assumption.

The number and distribution of sample trees must be considered in choosing a representative sample from the background stand. Sample size is dependent on the size of the background stand and on practical constraints on sampling. Preliminary computer simulations to test the effects of sample size on estimates of d suggest that 50 to 100 trees is a minimum for adequately estimating d. The distribution of these trees should be such that all background sources of pollen are well represented. Even though pollen can travel considerable distances, it is likely that dominant and codominant trees close to the orchard will contribute the majority of contaminating pollen an orchard receives. Thus, for practical purposes, sampling should be restricted to these trees.

A large sample approximation of the variance of $\hat{m}$ is:

$$\mathrm{var}(\hat{m}) = \frac{b(1-b)}{nd^2} \qquad (6)$$

where

n = number of seed orchard embryos sampled to estimate b.

This must be considered a minimum variance because it does not take into account the fact that d is estimated. Since $\mathrm{var}(\hat{m})$ is directly proportional to $1/d^2$, it is highly sensitive to the magnitude of d.

ILLUSTRATION OF THE MULTILOCUS TECHNIQUE

Use of the multilocus technique is illustrated with data from the Beaver Creek (BC) seed orchard. The first heavy cone crop in the BC orchard was in 1980 (the year of sampling) when the average age of clones in the orchard was 14 years. The orchard is surrounded by a large, essentially continuous stand of Douglas-fir. No pollen dilution zones, either between adjacent blocks or between the orchard blocks and the surrounding natural stand, are present.

Pollen contaminants in any one BC block could come from other orchard blocks or from the natural stand. Ideally, allele frequencies used in estimating d should be based on a representative sample of genotypes in both background sources. At BC, however, genotypes of all clones in all blocks were already known. For each block the allele frequencies in all remaining blocks were very similar to those among a sample of 183[2/] trees from the natural stand. Therefore, instead of randomly sampling ramets in other blocks, background stand allele frequencies for each block were calculated as unweighted means of the frequencies in other blocks and the natural stand.

Multilocus estimates (based on 14 allozyme loci) of pollen contamination from all background sources for each of three blocks and for all ten blocks combined are given in Table 2. For example, of 259 seeds sampled in block 7, 47 were found to have pollen gametes with multilocus genotypes which could not have come from any clone in the block (i.e., $\hat{b} = 47/259 = 0.181$). Furthermore, d is estimated to be 0.423 indicating that approximately 42.3 percent of the pollen gametes produced by all background sources have multilocus markers. Thus, total contamination in block 7 is estimated to be 0.181/0.423 = 0.43. The average level of pollen contamination over all ten blocks was estimated to be 0.52. Although this estimate seems high, it is not unreasonable, given the low level of pollen production in the orchard. An estimate of pollen contamination in an older Dougas-fir orchard (20

[2/] Genotypes of trees were inferred from a sample of seeds or determined directly from bud tissues. Of the 14 loci scored in seeds, only 8 could also be scored in buds. Thus, numbers of trees genotyped per locus ranged from 57 (6 loci) to 183 (8 loci).

Table 2.--Multilocus estimates of pollen contamination from all background sources ($\hat{m}$, other blocks and surrounding natural stand) and from the surrounding natural stand only ($\hat{m}_s$) in three blocks, and all ten blocks combined, at the Beaver Creek Douglas-fir seed orchard.[a]

Orchard block	Clones	All sources[c]				Natural stand only[c]		
		N[b]	$\hat{b}$	$\hat{d}$	$\hat{m}$ (SE)	$\hat{b}_s$	$\hat{d}_s$	$\hat{m}_s$ (SE)
BC-7	25	259	.181	.423	.43 (.057)	.031	.112	.28 (.096)
BC-5	25	582	.175	.366	.48 (.043)	.048	.112	.43 (.079)
BC-10	27	542	.207	.323	.64 (.054)	.044	.112	.39 (.079)
All blocks combined	251	3023	--	--	.52[d] (.061)	.044	.112	.39 (.033)

[a] Based on 14 allozyme loci.

[b] N = number of pollen gametes (seeds) sampled.

[c] $\hat{b}$ and $\hat{b}_s$ are the estimated proportions of orchard ovules fertilized by pollen gametes with multilocus markers from all background sources and from the natural stand, respectively. $\hat{d}$ and $\hat{d}_s$ are the estimated proportions of multilocus markers in the pollen of all background sources and in the pollen of the surrounding stand, respectively.

[d] Unweighted mean over all blocks.

years) which has been producing heavy pollen and cone crops periodically since 1971, was much lower ($\hat{m}$ = 0.29).

The multilocus technique was also used to determine the amount of pollen contamination in each block from the natural stand only. First, the proportion of pollen gametes in the seed sample of each block which could not have come from any of the orchard blocks was determined ($\hat{b}_s$ in Table 2). Then, allele frequencies in the natural stand were used to calculate $\hat{d}_s$, and $\hat{m}_s$ was estimated as $\hat{b}_s/\hat{d}_s$ (Table 2). Pollen from the surrounding natural stand accounted for a large proportion of the total contamination in BC blocks 5, 7, and 10. Over all the blocks, pollen from the natural stand ($\hat{m}_s$ = 0.39) made up 75 percent of the total contamination ($\hat{m}$ = 0.52). The high proportion of contamination from the natural stand again seems reasonable given the low level of pollen production in the orchard. As the orchard ages and pollen production within each block increases, it is likely that both total contamination and the proportion of contamination due to pollen from the natural stand will decrease.

As the number of clones in an orchard increases, the ability to detect pollen contaminants will decrease because fewer multilocus pollen genotypes in background sources will differ from those produced by the orchard clones. Nevertheless, when all 251 clones at BC are considered together, a moderate proportion ($\hat{d}_s = 0.112$) of the pollen in the surrounding stands is expected to have marker genotypes. Thus, even in an orchard with large numbers of clones or with small values of d, it is possible to use the multilocus technique to estimate m. However, larger sample sizes would be required to maintain low standard errors.

CONCLUSIONS AND RECOMMENDATIONS

The multilocus method of estimating pollen contamination in clonal seed orchards has several advantages over single-locus methods described previously (Friedman and Adams 1981). Because a large proportion of contaminants are observed directly, multilocus estimates are more efficient (i.e., have lower standard errors) than single-locus estimates. Furthermore, unlike single-locus methods, the multilocus method does not require differences in allele frequency between the orchard and background stand. Finally, both methods require estimates of allele frequencies in the background stand. Frequencies of a number of multilocus markers are combined to estimate d in the multilocus method. Thus, $\hat{d}$ is not likely to be very sensitive to factors such as unequal pollen production, gametic selection or genetic subdivisions in the natural stand, all of which might cause single-locus marker frequencies in pollen to differ considerably from those in adult trees.

Although we are still testing the multilocus technique, some preliminary recommendations for its use can be made:

1. Multilocus genotypes of all clones in the orchard and a sample of trees from the background stand are necessary to estimate d. Unless radical changes in the composition of the orchard or background stand are made, d need only be calculated once. Levels of pollen contamination in subsequent years or after application of different pollen management techniques can then be determined by estimating b from a sample of the seed crop and dividing it by the previously estimated d.

2. Based on preliminary computer simulations, a sample of at least 50 to 100 dominant or codominant trees in the background stand is a minimum for adequately estimating d.

3. The availability of variable loci and the degree of precision required dictate the number of loci to use in estimating m. The magnitude of d decreases as the number of loci decreases. In BC block 5, estimates of m were similar using 14 or 9 loci but the standard error of the estimate based on 9 loci was approximately 23 percent larger. Thus, to maintain a certain level of precision with fewer loci, the sample of seeds in the orchard crop must be increased.

4. The number of seeds to sample in the orchard crop depends on the size of d and the degree of precision required. In the absence of previous knowledge of the magnitude of m, we suggest that sequential sampling be employed, with sample size progressively increased until the desired level of precision is reached.

LITERATURE CITED

Adams, W. T. 1982. Application of isozymes in tree breeding. In S. D. Tarksley and T. J. Orton (eds.), Isozymes in plant genetics and breeding. Elsevier Scientific Publ. Co. (in press).

Bridgwater, F. E., and Trew, I. F. 1981. Supplemental mass pollination. In E. C. Franklin (ed.), Pollen management handbook, pp. 52-57. USDA Agric. Handb. 587. Washington, D.C.

Brown, A. H. D., and Moran, G. F. 1981. Isozymes and genetic resources of forest trees. In M. T. Conkle (technical coordinator), Proc. Symp. Isozymes of North Am. Forest Trees and Forest Insects, pp. 1-10. Berkeley, CA. USDA Forest Serv. Gen. Tech. Rep. PSW-48.

Denison, N. P., and Franklin, E. C. 1975. Pollen management. In R. Faulkner (ed.), Seed orchards, pp. 92-100. Forest. Comm. Bull. No. 54. Her Majesty's Stationery Office, London.

Friedman, S. T., and Adams, W. T. 1981. Genetic efficiency in loblolly pine seed orchards. Proc. 16th South. Forest Tree Improv. Conf., Blacksburg, VA. pp. 213-224.

Schmidt, R. L., and Hamblett, K. C. 1962. Directional sources of extraneous pollen at three seed orchard sites on Vancouver Island. For. Chron. 38(2): 203-207.

Silen, R. 1962. Pollen dispersal considerations for Douglas-fir. J. For. 60:790-795.

Silen, R., and Keane, G. 1969. Cooling a Douglas-fir seed orchard to avoid pollen contamination. USDA Forest Serv. Res. Note PNW-101.

Spiess, E. R. 1977. Genes in populations. 780 p. John Wiley and Sons, Inc.

Squillace, A. E. 1967. Effectiveness of 400-foot isolation around a slash pine seed orchard. J. For. 65:823-824.

Squillace, A. E., and Long, E. M. 1981. Proportion of pollen from non-orchard sources. In E. C. Franklin (ed.), Pollen management handbook, pp. 15-19. USDA Agric. Handb. 587. Washington, D.C.

Wang, C. W., Perry, T. O., and Johnson, A. G. 1960. Pollen dispersion of slash pine (*Pinus elliottii* Engelm.) with special reference to seed orchard management. Silvae Genet. 9:78-86.

FEASIBILITY OF SUPPLEMENTAL MASS POLLINATION TO INCREASE GENETIC GAINS FROM SEED ORCHARDS

F. E. Bridgwater and C. G. Williams[1]

Abstract.--Dyed pollen was applied to unprotected clusters of female strobili of three clones in a mature, loblolly pine, (*Pinus taeda* L.), seed orchard. Single and multiple pollinations were made as strobilus receptivity progressed. Dissection of ovules on strobili collected after the pollination season was past revealed that supplemental mass pollination to increase genetic gains is feasible with proper timing and application. The best average percentage of dyed pollen in ovules of the three clones was 92% for multiple pollinations. An average of 86% dyed pollen was introduced into pollen chambers of the three clones with a single application when strobili were at maximum receptivity.

Additional keywords: Supplemental mass pollination, *Pinus taeda*, genetic gain.

INTRODUCTION

Supplemental mass pollination is the broadcast application of pollen to strobili that are not isolated from wind-borne pollen. Potential benefits from supplemental mass pollination in conventional intraspecific tree improvement programs are increases in the yield of sound seeds and in realized genetic gains. Filled seed yields can be improved in loblolly pine seed orchards under certain conditions (Bridgwater and Bramlett 1982). However, the feasibility of supplemental mass pollination to increase genetic gains has not been demonstrated.

Genetic gains may be increased in established seed orchards through supplemental mass pollination only if supplemental pollen can be introduced into ovules in sufficient numbers to compete with wind-borne pollen.

METHODS

In this study we quantified the numbers and proportions of wind-borne and supplemental pollen grains in pollen chambers of three loblolly pine clones in a mature seed orchard.[2] The study was conducted during the springs of 1980 and 1981 when the seed orchard was 20 and 21 years from grafting, respectively. Treatments were applied to varying numbers of strobili in clusters on one ramet of each of three clones. Different ramets were used in the two study years.

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[2] Weyerhaeuser Company's J. P. Weyerhaeuser First Generation Piedmont Seed Orchard near Washington, North Carolina.

Dyed pollen grains were used in supplemental pollinations. These were easily distinguished from wind-borne pollen (which had not been dyed) when ovules were dissected. The procedures used for dissections were essentially those of Matthews and Blalock (1981). Dyed pollen was applied as strobilus receptivity progressed from stage 3 through stage 5 late (Bramlett and O'Gwynn 1981). Four supplemental pollination schedules (treatments) were used in the 1980 study. The first schedule consisted of four applications of dyed pollen at receptivity stages 3, 4, 5 and 5 late. Each of the three remaining treatments began successively one stage later, that is, 4 + 5 + 5 late, 5 + 5 late, and 5 late. Treatments in the 1981 study were done in the same fashion but included one more stage of strobilus development so that treatment schedules were 3 + 4 + 4 late + 5 + 5 late, 4 + 4 late + 5 + 5 late, 4 late + 5 + 5 late, 5 + 5 late and 5 late. Also, in the 1981 study a series of single supplemental pollinations were made at each of the 5 successive stages of strobilus receptivity. One to several clusters of strobili were selected for wind-pollinated checks in each study to quantify the levels of wind-borne pollen.

Pollen applications were made from a plastic squeeze bottle with a small tube extending from the top whereby the pollen spray was directed onto individual strobili. Pollen amounts were not quantified. Dyed pollen was simply applied until it could be seen on all surfaces of the strobilus. To accomplish the delivery of the same quantities of pollen in an operational application of supplemental pollen would probably be uneconomic if not impossible. However, the objective of this trial was to test the feasiblity of supplemental mass pollinations, not its practicality.

Fifteen ovules from each of three cones representing each clone x treatment cell were dissected in the 1980 study. Nine ovules from each of five cones were sampled from each clone x treatment cell in the 1981 study. In both studies, one of the two ovules per scale was dissected. One-third of the scales came from each of the distal, medial, and proximal parts of the strobilus. The numbers of dyed and wind-borne pollen grains were counted for each dissected ovule.

Standard analysis of variance procedures were used to partition the variance among clones, treatments, cones in clones x treatment cells, ovules in cones and the interaction between clones and treatments and to test hypotheses. Duncan's multiple range tests were used to group values not significantly different at the 95% confidence level.

RESULTS AND DISCUSSION

The trait of primary interest, percentage of supplemental (dyed) pollen grains per ovule, differed significantly among clones and treatments in both studies. The percentage of dyed pollen grains theoretically estimated the proportion of ovules that will produce a seed resulting from fertilization by a supplemental pollen grain. We assumed that the wind-borne and supplemental pollen are both 100% viable and there are no differential genetic effects.

Two applications of supplemental pollen (5 + 5 late) beginning at the stage of maximum receptivity (stage 5) was the best, multiple-pollination treatment in both the 1980 and 1981 studies (Tables 1 and 2). Average percentages of dyed pollen for all three clones for treatment 5 + 5 late were 72% and 92% in 1980 and 1981, respectively. This result was unexpected. It seemed reasonable at the outset of the study that treatment schedules which began earlier and thus had more applications of supplemental pollen would have the highest percentages of dyed pollen. Had this been the case, the effects of a single application of pollen at any receptivity stage could have been determined by substraction. It became apparent that this simple system was not in operation upon examination of the results of the 1980 study (Table 1). In fact, the observed trend was the opposite of that which was expected. Thus, we added the series of single applications in 1981 as well as repeated the series of multiple treatments. Again, in the 1981 study, the expected trend for multiple pollinations was not realized. The reasons for this unexpected trend are not known. However, this puzzling result is primarily of academic interest since the simplest, least intensive treatment (5 + 5 late) was best in both years. A single application of supplemental pollen at maximum receptivity was nearly as effective as the best multiple-pollination treatment. We realized 86% dyed pollen in pollen chambers with a single application at strobilus receptivity stage 5. The trend in the series of single-application treatments was as expected. The proportion of dyed pollen grains per ovule increased as the treatments were applied closer and closer to full receptivity. The proportion dropped off markedly just after maximum receptivity (Table 3.)

Table 1.--Results from the 1980 Supplemental Mass Pollination Trial.

Treatment Differences

Supplemental Pollen Applied at Flower Stage(s)	Mean % Supplemental Pollen In Pollen Chambers	Mean Total Numbers (Wind + Supplemental) Pollen In Pollen Chambers
5 + 5 Late	72% a[1/]	6.5 a
4 + 5 + 5 Late	67% ab	6.2 a
3 + 4 + 5 + 5 Late	59% b	5.5 ab
5 Late	30% c	5.2 b
Wind Pollinated Only		4.7 b

Clonal Differences For the Best (5 + 5 Late) Treatment Above

Clone	Mean % Supplemental Pollen In Pollen Chambers
8-118	84% a[1/]
8-107	74% a
8-126	58% b

[1/] Means followed by the same letter are not significantly different at the 95% confidence level.

Table 2.--Results from the multiple-pollination treatments in the 1981 Supplemental Mass Pollination Trial.

Differences Among Multiple-Pollination Treatments

Supplemental Pollen Applied at Flower Stage(s)	Mean % Supplemental Pollen In Pollen Chambers	Mean Total Numbers (Wind + Supplemental) Pollen In Pollen Chambers
5 + 5 Late	92% a[1]	5.4 a
3 + 4 + 4 Late + 5 + 5 Late	84% a	4.9 abc
4 Late + 5 + 5 Late	72% ab	5.4 a
4 + 4 Late + 5 + 5 Late	71% ab	5.2 ab
5 Late	55% b	4.1 bc
Wind Pollinated Only		3.8 c

Clonal Differences For The Best (5 + 5 Late) Treatment Above

Clone	Mean % Supplemental Pollen In Pollen Chambers
8-118	98% a
8-126	93% b
8-107	80% b

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[1] Means followed by the same letter are not significantly different at the 95% confidence level.

Table 3.--Results from the single-pollination treatments in the 1981 Supplemental Mass Pollination Trial.

Differences Among Single-Pollination Treatments

Supplemental Pollen Applied at Flower Stage(s)	Mean % Supplemental Pollen In Pollen Chambers	Mean Total Numbers (Wind + Supplemental) Pollen In Pollen Chambers
5	86% a[1]	5.5 a
4 Late	68% a	5.2 ab
5 Late	55% ab	4.1 bc
4	39% ab	4.7 abc
3	2% b	4.0 c
Wind Pollinated Only		3.8 c

Clonal Differences For The Best (5 + 5 Late) Treatment Above

Clone	Mean % Supplemental
8-118	100% a[1]
8-126	84% b
8-107	73% b

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[1] Means followed by the same letter are not significantly different at the 95% confidence level.

The timing of applications of supplemental pollen was apparently critical. Beginning applications before maximum receptivity (stage 5) reduced the expected proportions of seeds from supplemental pollen in both cumulative and the single application series (Tables 1, 2 and 3). The reduction was even greater when application was made after maximum receptivity had passed (5 late).

The timing of supplemental pollinations is also critical because pollen applied to strobili first has the best chance of producing seeds (Franklin 1974). Thus, if wind-borne pollen arrived before supplemental pollen, the predicted proportions of seeds from supplemental pollination may be overestimated in this experiment. It was not possible in the dissection process to determine whether dyed or wind-borne pollen had a positional advantage on the nucellus. The proportions of seed from supplemental pollen may be overestimated in this experiment for another reason. A comparison of total number of dyed + wind-borne pollen in pollen chambers to the number in wind-pollinated check ovules (Tables 1, 2 and 3) shows that there was always more pollen in pollen chambers that contained dyed pollen. Furthermore, the total number of pollen grains increased as the proportion of dyed pollen increased. This suggested that dyed pollen grains may have been smaller than wind-borne pollen and thus it was possible to put more of them into pollen chambers. Therefore, their proportionate numbers would be greater than if they had not been dyed. The magnitude of this overestimate (if it exists) was probably small. We did not measure pollen grains in this experiment. However, other workers report that the numbers of pollen grains in a volume of pollen dyed in alcohol-soluble dyes is 10% greater than in equal volumes of pollen that had not been dyed (Personal Communications, Dr. M. S. Greenwood, Weyerhaeuser Co., Hot Springs, AR).

The best treatments in the three series should still result in substantially large numbers of seeds from supplemental pollen, even though the porportion of seeds expected from supplemental pollen may have been overestimated. In the best 1980 treatment (5 + 5 late), 24% of the dissected ovules contained only supplemental pollen. Seventy-nine percent of the ovules contained greater than 50% supplemental pollen thus the supplemental pollen had a numerical advantage. The best multiple-application treatment in 1981 (5 + 5 late) had 63% of ovules which contained only supplemental pollen and 87% with more than 50% supplemental pollen. The best single-application treatment (stage 5) had 73% ovules with only dyed pollen and 96% that contained more than 50% dyed pollen.

There were statistically significant differences among the three clones for the best treatment in each of the three treatment series (Tables 1, 2 and 3). There were no meaningful interactions between clones and treatments. In other words, multiple pollinations at stages 5 + 5 late or a single pollination at stage 5 was best (or not significantly poorer than the best treatment) for all three clones in all three treatment series. Clones 8-107 and 8-126 changed ranks in the 5 + 5 late treatment in the two study years. This was probably due to the variance introduced by relying upon a subjective determination of the appropriate strobilus receptivity stage for application.

CONCLUSIONS AND RECOMMENDATIONS

Genetic gains can be increased through supplemental mass pollinations. Success depends upon pollen application when female strobili are at maximum receptivity.

Supplemental pollination was most successful when two successive applications were made at strobilus receptivity stages 5 and 5 late. The best single application was made at stage 5, or maximum receptivity. Earlier or later applications reduced the percentage of supplemental pollen in pollen chambers.

This study clearly demonstrated the importance of precise timing of supplemental pollinations. However, we did not control pollen amounts. Rather, we applied large amounts of supplemental pollen to individual strobili to determine the feasibility of supplemental mass pollinations. If such large amounts of pollen were used in a large-scale operation, the system might not be economical. Further research should be done to quantify success in operational systems.

LITERATURE CITED

Bramlett, D. L. and C. H. O'Gwynn. 1981. Controlled pollination. In: Pollen Management Handbook. U.S.D.A., For. Ser., Agricultural Handbook No. 587, pp. 44-51.

Bridgwater, F. E. and D. L. Bramlett. 1982. Supplemental mass pollination to increase seed yields in loblolly pine seed orchards. S. Jour. of App. For., Vol. 6, No. 2, pp. 100-104.

Franklin, E. C. 1974. Pollination in slash pine: first come, first served. In: Proc. Colloq. on Seed Yield From S. Pine Seed Orchards. Ga. For. Res. Council, Macon, Ga. pp. 15-20

Matthews, F. R. and T. E. Blalock. 1981. Loblolly pine pollen grain counts by ovule dissection. In: Proc. of the 16th Southern Forest Tree Improvement Conf., Virginia Polytechnic Institute and State Univ., Blacksburg, Virginia, May 27-28, 1981, pp. 276-278.

POLLINATION SUCCESS IN RELATION TO FEMALE FLOWER DEVELOPMENT IN LOBLOLLY PINE

by

David L. Bramlett and Frederick R. Matthews[1/]

Abstract.--The proper timing of control pollinations is a major element of a successful pine breeding program. Frequently, phenological variability requires (1) pollinations to be completed at times other than maximum female receptivity (stage 5) or (2) multiple pollinations of the same flowers. In this study, single pollinations were completed at 2-day intervals from March 14-25. In addition, multiple pollinations were completed in combinations of flower developmental stages before, during, and after stage 5. Success of the pollination was evaluated by removing sample conelets 2 weeks after pollen application and counting the pollen grains in the pollen chamber of 10 ovules of each conelet. Results indicated that the largest number of pollen grains are found in ovules pollinated at stage 5. However, only slight, non-significant reductions were observed in flowers pollinated 2 days before or 2 days after stage 5. Very early or very late pollintions had significantly fewer pollen grains per ovule. Multiple pollinations were not significantly different from ovules pollinated at only stage 5.

Additional keywords: control pollination, tree breeding, seed orchard, pollen.

A continuing concern among tree breeders is the correct timing of pollen applications to female flowers. Several studies have evaluated this question, and the general consensus is that stage 5 as described by Cumming and Righter (1948) is the optimum time for controlled pollination. Tree breeders, however, may not always be able to pollinate at precisely stage 5. Uncontrolled events, such as atypical spring weather or clonal variation, may result in less than optimum timing of the pollination. Breeders, therefore, ask whether pollinaton success is affected if (1) pollen is applied when receptivity is less than optimum, or (2) if pollen is applied at more than one time to an individual bag? The study reported here addressed these questions.

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METHODS

Treatments in the study were seven timings of single pollinations ranging from female flowers at stage 3 to flowers in stage 6; multiple pollinations of four combinations of the single applications; and, a wind-pollinated control. Two ramets of each of four loblolly pine (Pinus taeda L.) clones in the Georgia Forestry Commission's Arrowhead Seed Orchard were selected as female parents. On each tree, two replications of the 12 timing treatments were installed. Each timing treatment was applied to an individual branch having from one to seven female flowers. Isolation bags were placed on the branches March 1, 1982 and treatments randomly assigned to each branch. Pollination treatments were:

TREATMENT NO.	DESCRIPTION	FLOWER STAGE
1	Very, very early	3.0
2	Very early	4.0
3	Early	4.5
4	Maximum	5.0
5	Late	5.5
6	Very late	5.8
7	Very, very late	6.0
8	Early + maximum	4.5 + 5.0
9	Early + late	4.5 + 5.5
10	Maximum + late	5.0 + 5.5
11	Early + maximum + late	4.5 +5.0 + 5.5
12	Wind	--------

The pollen source was a five-clone polymix of equal volumes from unrelated loblolly pine clones in the Arrowhead Seed Orchard. Pollen was collected in 1981 and stored under vacuum until pollination. The pollen was applied with a cyclone pollinator (Matthews and Bramlett 1980) when flower stages approximated the treatment description.

Bags were removed and conelets collected 2 weeks after pollination. A single conelet from each treatment was collected from each ramet. Ten ovules on each conelet were dissected under a microscope, the nucelli with the pollen attached were removed, and grains were counted (Matthews and Blalock 1981). In all, 960 ovules were examined.

RESULTS AND DISCUSSION

Single Pollinations

In central Georgia in early March of 1982 pine flowers developed rapidly during several continuous days of warm and sunny weather. The controlled pollinations began on March 12 when flowers in the earliest clone had emerged from the bud scales and were in stage 3. Ovules from flowers that were pollinated in stage 3 had an average of 1.15 pollen grains per ovule (Table 1). Two days later, the flowers had developed to stage 4, with approximately one half the ovule-bearing scales exposed. Pollinations at stage 4 produced an average of 1.93 pollen grains per ovule. One or two days later, flowers were in mid stage 4 and had extended to 3/4 of the stage 5 flower size. Ovules from stage 4.5-pollinated flowers averaged 2.89 pollen grains per ovule.

Flowers in the isolation bags reached maximum receptivity (stage 5), as indicated by the complete emergence and extension of the flower from the bud scales, 4 to 5 days after stage 3 began. At this developmental stage, the scales are at approximate right angles to the cone axis and the maximum opening between the scales and the bracts offers the greatest access for pollen. Ovules from flowers pollinated at stage 5 had the highest observed pollen count, averaging 3.71 pollen grains per ovule.

Pollinations 2 days after flowers were in stage 5 were still effective, depositing 3.16 pollen grains per ovule. However, 4 days after stage 5, flower receptivity had markedly decreased and only 0.26 pollen grains were observed in the pollinated ovules. Receptivity decreases as the scales increase in thickness and the opening between the scale and the bract is reduced, restricting the pollen flow to the ovules. Seven days after maximum receptivity, the flowers were in stage 6 in three of the four clones and pollinations produced 0.0 pollen grains per ovule. In one clone (506) a few ovules were pollinated, but pollination at this stage is not practical.

Multiple Pollinations

Although it is generally agreed that pollen should be applied at maximum receptivity, variability of flower development within individual bags may make it difficult to decide when to pollinate. In these cases, many breeders have used multiple pollinations of the same bag. In this study double and triple combinations of early, maximum, and late pollinations were also evaluated.

Multiple pollinations were very effective; all double and triple applications produced more than three pollen grains per ovule. However, the multiple combinations were not significantly better (0.05 level of probability) than single applications at the same flower development stages used for the combinations. Multiple pollinations in very early or very late stages of flower development were not tested.

Table 1.--Number of pollen grains per ovule observed in loblolly pine following pollination at varying development stages

POLLINATION TIME	FLOWER STAGE	POLLEN GRAINS PER OVULE CLONE 506	523	557	630	AVG 1/
Single Application						
Very, very early	3.0	1.10	0.60	1.85	1.05	1.15 b
Very early	4.0	2.15	2.70	0.95	1.90	1.93 b
Early	4.5	3.25	3.55	2.80	1.95	2.89 a
Maximum	5.0	3.40	4.70	2.95	3.80	3.71 a
Late	5.5	2.85	3.40	3.85	2.85	3.24 a
Very late	5.8	0.20	0.15	0.25	0.45	0.26 c
Very, very late	6.0	0.40	0.00	0.00	0.00	0.10 c
Double Application						
Early + maximum	4.5 + 5.0	2.60	4.05	2.80	2.60	3.01 a
Early + late	4.5 + 5.5	3.50	3.45	3.20	2.40	3.14 a
Maximum + late	5.0 + 5.5	3.15	4.65	2.15	3.65	3.39 a
Triple Application						
Early+max+late	4.5+5.0 + 5.5	2.85	3.70	3.65	2.75	3.24 a
Wind Pollinated		3.15	4.10	4.05	3.90	3.80 a

1/ Mean values with the same letters are not significantly different (0.05 level).

Wind Pollinations

Ovules from wind-pollinated conelets consistently had the highest number of pollen grains per ovule and averaged 3.80 for all four clones. This value was not significantly higher than those for early, maximum, late, or multiple pollintions. A high pollen count, however, is to be expected in conelets that are exposed to a high density of pollen during many days of pollen flight from varying directions. In dissection of the conelets and ovules, large quantities of excess pollen were found between the scales of the conelets that had been control pollinated at receptive stages. Similar quantities of pollen were not observed in wind-pollinated conelets.

RECOMMENDATIONS AND CONCLUSIONS

Although stage 5 appears to be the optimum time to pollinate, pollinations can be successful within ± 2 days from maximum receptivity. We recommend pollen application during this period.

Multiple pollinations did not significantly increase the pollen count per ovule when compared to a single application at stage 4.5, 5.0, or 5.5. Such treatment may be profitable, however, in bags where flowers vary widely in stage of development.

LITERATURE CITED

Cumming, W. C., and F. I. Righter. 1948. Methods used to control pollination of pines in the Sierra Nevada of California. U.S. Dep. Agric., Circ. 792, 10 p., Washington, D.C.

Matthews, Fred R., and Tony E. Blalock. 1981. Loblolly pine pollen grain counts by ovule dissection. *In* Proc. 16th South. For. Tree Improv. Conf., May 27-28, 1981: 276-278, Blacksburg, VA.

Matthews, Fred R., and David L. Bramlett. 1981. Cyclone pollinator improves loblolly pine seed yields in controlled pollinations. Sou. J. Appl. For. 5: 42-46.

SELECTION AND BREEDING STRATEGIES

A TREE IMPROVEMENT PROGRAM FOR SOUTHERN HARDWOODS[1]

R. C. Purnell and R. C. Kellison[2]

Abstract.--The hardwood genetics program started by the North Carolina State University-Industrial Cooperative Hardwood Research Program[3] has undergone changes which have produced groups of selected trees with different levels of improvement. The time has come to integrate the groups into a comprehensive improvement program. Only a few organizations are establishing greater than 800 hectares of hardwood plantations annually. The best option for an improvement program with limited interest is to rely upon an open-pollinated breeding scheme. The breeding population within each breeding region will be subdivided into 10 to 15 subgroups. Each subgroup's planting will be designed to improve the chances for cross-pollination between families within the subgroup. Open-pollinated progeny from the best individuals in these plantings will be used for the next generation's breeding population. Clonal seed orchards will be established, using the best trees from each subgroup within a region. Accompanying the seed orchard program will be an experimental vegetative propagation program with anticipation that vegetative popagules will eventually supplement or replace seedlings in reforestation.

INTRODUCTION

Hardwoods have been planted just as long as pines in the southern United States; however, most hardwoods planted before 1970 failed. The failure was largely due to misguided attempts to force the hardwoods to respond to silvicultural practices developed for the southern pines. Even during the 1960s when great interest existed in planting southern hardwoods, the silvicultural practices necessary for successful plantation establishment were poorly understood. Most successful commercial hardwood plantations were established after 1970, when intensive cultural practices became the standard. About 40,000 hectares of successful hardwood plantations exist in the southern United States, and the area is increasing by approximately 4,000 hectares annually. With any plantation program it is imperative that each hectare be planted with the best genetically available stock and that a comprehensive improvement program be conducted to provide that stock.

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[1] Presented at the 17th Southern Forest Tree Improvement Conference, University of Georgia, Athens, June 6-9, 1983.

[2] Graduate Research Assistant and Director, respectively, Hardwood Research Cooperative, School of Forest Resources, N. C. State University, Raleigh,

[3] The Hardwood Research Program consists of 18 industrial and 2 public organizations who own or control about 6 million hectares of land. Major emphasis of the cooperators is pine plantation establishment and management. About 10% of their effort is on regeneration and management of natural hardwood stands. Only 20% of the cooperators are planting hardwoods on a commercial scale.

Site specificity of most southern hardwood species dictates that four or five species must be used in an operational plantation program. As a result, the improvement program must to some degree genetically improve all the species needed in the plantation program. The degree of genetic improvement for a species will be determined by the economic value, unique inheritance patterns, and biological characteristics of the species. The decision could ostensibly be to establish intensive improvement programs for some species and less intensive improvement programs for other species. The improvement program outlined in this paper and adopted by the members of the N. C. State University-Industry Cooperative Research Program is sufficiently general so that it can be adapted to the needs and objectives for each species.

TREE IMPROVEMENT PROGRAM

Intensive Selection--Clonal Seed Orchard Programs

The hardwood tree improvement program has undergone some modifications since its initiation by the Hardwood Research Cooperative in 1963. The initial program emphasized selecting superior phenotypes ranging in age from 25 to 65 years old from natural stands, using a selection index. The index combined heritability and economic importance of selected traits into one score that was used to judge the relative quality of graded trees according to species and site. The traits used in the index were volume, pest resistance, crown conformation, leader dominance, bole straightness, bole pruning, freedom from epicormic branching, and branch angle. This system was used in lieu of a comparison tree or "check" tree selection system because most commercially important southern hardwoods occur in mixed stands where comparison selection systems are inappropriate.

A total of 709 trees representing 27 species were selected, using the index system. Many of the select trees were preserved in clone banks, while superior sweetgum (*Liquidambar styraciflua* L.), sycamore (*Platanus occidentalis* L.), yellow-poplar (*Liriodendron tulipifera* L.), and green ash (*Fraxinus pennsylvanica* Marsh.) were used to establish clonal seed orchards (Table 1). The progeny from these selected trees have been included in open-pollinated genetic tests.

Extensive Selection--Open-Pollinated Genetic Tests

The selection of phenotypically superior southern hardwood trees that were also genotypically superior was difficult because natural hardwood stands are composed of many species and have originated from both seedlings and sprouts. Trees from sprout origin are often selected at the expense of trees from seedling origin because sprouts have superior bole and crown characteristics which are features of vegetative propagules (Sweet and Wells, 1974). Phenotypic selection is also difficult in hardwood stands because many stands have suffered from dysgenic selection that has resulted from repeated, incomplete harvests.

Table 1.--Hardwood seed orchards established by members of the N. C. State Hardwood Research Program

Species	Orchards Established	Area (Hectares)	Clones Grafted (Number)
Sycamore	7	5.7	130
Sweetgum	5	13.0	70
Yellow-Poplar	1	2.4	22
Green Ash	1	1.6	17
Water-Willow Oak	2	2.4	[a]

[a] Seedling seed orchards

The Hardwood Research Cooperative is circumventing these problems and limitations by selecting trees that have above-average phenotypic value for that site but not necessarily meeting the phenotypically superior standard required by the index selection. The genotypic value of the above-average trees is then determined in open-pollinated genetic (mother-tree) tests. Information from these tests will then be used to identify the best trees for grafting into clonal seed orchards. Using this extensive selection system, an additional 507 trees from six commercially important hardwood species are being tested in open-pollinated genetic tests (Table 2).

Table 2.--Number of above-average phenotypes being tested in open-pollinated genetic tests

Species	Trees Being Tested
Sycamore	231
Sweetgum	213
Water-Willow Oak	31
Black Walnut	38
European Alder (*Alnus glutinosa*)	32

THE FUTURE

The need exists to meld the trees selected and tested in the intensive and extensive selection programs into a cohesive improvement program. Despite the large number of species that are represented by selected trees, only sycamore, sweetgum, green ash, water oak (*Quercus nigra* L.) and willow oak (*Q. phellos* L.) have enough commercial importance across the southern United States to warrant a regional program. Other species that have great local commercial importance, such as yellow-poplar in the Southern Appalachians and cottonwood (*Populus deltoides* Bartr.) in the Mississippi Delta, could be genetically improved by the same type of breeding scheme on a smaller scale.

A large investment has been made for the improvement of southern hardwoods, but only a few organizations are establishing greater than 800 hectares of plantations annually. The best option for an improvement program of limited interest is to rely upon an open-pollinated breeding scheme. An open-pollinated breeding scheme offers the opportunity for some genetic gain at a cost that is generally lower than a control-pollinated program, especially for species where floral biology is poorly understood. However, increasing relatedness and accompanying inbreeding depression may require a shift to more control-pollinated breeding in the future.

For maximum efficiency and genetic gain, a tree improvement program has two distinct phases -- a breeding phase and a production phase. The breeding phase allows continuing genetic improvement into advanced generations and the production phase allows mass production of improved material in seeds or vegetative propagules. The individuals used in the production phase are a subset of the best individuals from the breeding population.

Breeding Phase

To maintain genetic diversity and integrity of geographic seed sources, the southeastern United States has been divided into breeding regions for each commercially important species. The breeding regions are zones that have genetically similar trees and similar physiographic and environmental conditions. For example, the range of sweetgum east of the Mississippi River, the working territory of the Hardwood Research Cooperative, has been divided into seven breeding zones (Figure 1). The selected trees will be utilized only within the region from which they originate, until tests reveal their suitability out side the breeding region.

The cooperating organizations within each breeding region will continue to select and evaluate trees from natural stands and unimproved plantations, using the extensive selection methods until each breeding region has selected at least 500 above-average trees per species. The open-pollinated genetic tests of the 500 above-average trees established with the extensive selection method will be used to select the superior trees for the breeding population, based on family and individual tree information. The two best trees from the best 50% of the families will be the parents of the second-generation breeding population. The parents will be divided into groups of 50, and open-pollinated seed from each tree in the group will be kept together as a genetic test of the trees and as a subline of the second-generation population. Between 10 and 15 genetic tests will compose the breeding population for a breeding region and will be handled similarly to a sublined breeding population (McKeand and Beineke, 1980). Three commercial check lots common to each region will be included in all genetic tests of that region.

East genetic test will be planted at two locations, with each location having ten replications with six trees per family per replication. The six trees from each family in a replication will be divided into three groups of two, and the three groups will be scattered throughout the replication so that a different set of families will surround each group (Figure 2). The groups will allow for a 50% thinning in the tests without losing any families and will also improve cross-pollination among families. Genetic tests will be computer-designed from N. C. State University. The cycle will then be repeated for subsequent generations, with individuals selected for the next breeding population being chosen from the previous breeding population on the basis of family and individual tree information (Figure 3). The level of coancestry within each subline will increase each generation, and the genetic quality between the sublines

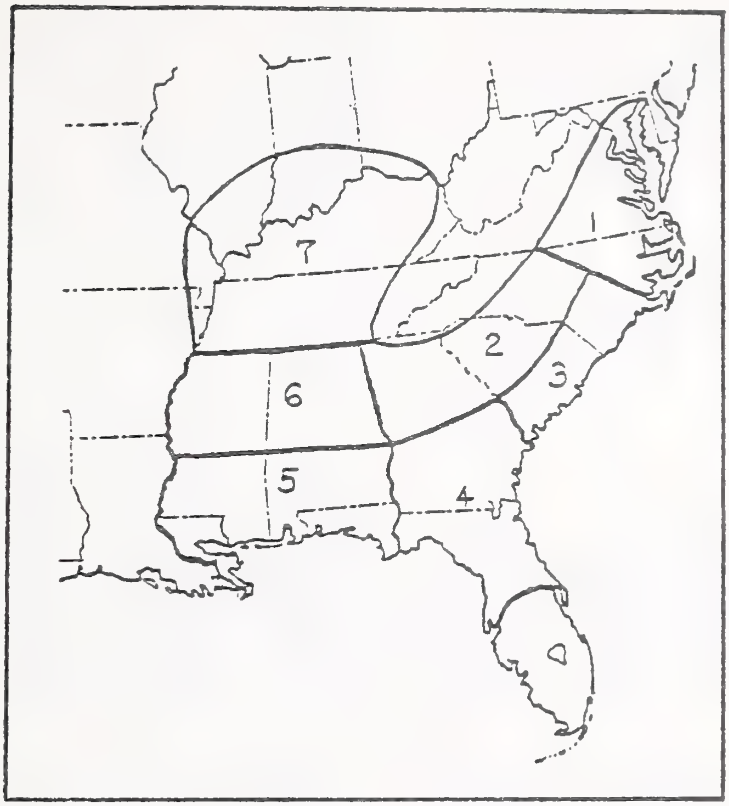
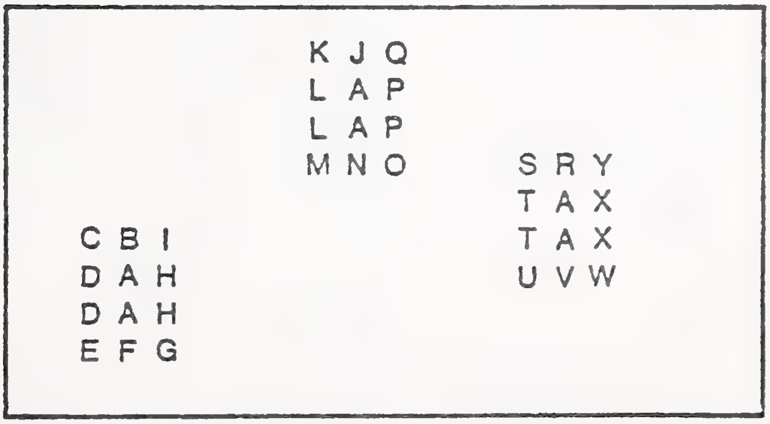


Figure 1.--Proposed breeding program for sweetgum.



i^{th} Replication

Figure 2.--Design of the 6-tree, partial-noncontiguous plots used in the second generation genetic tests.

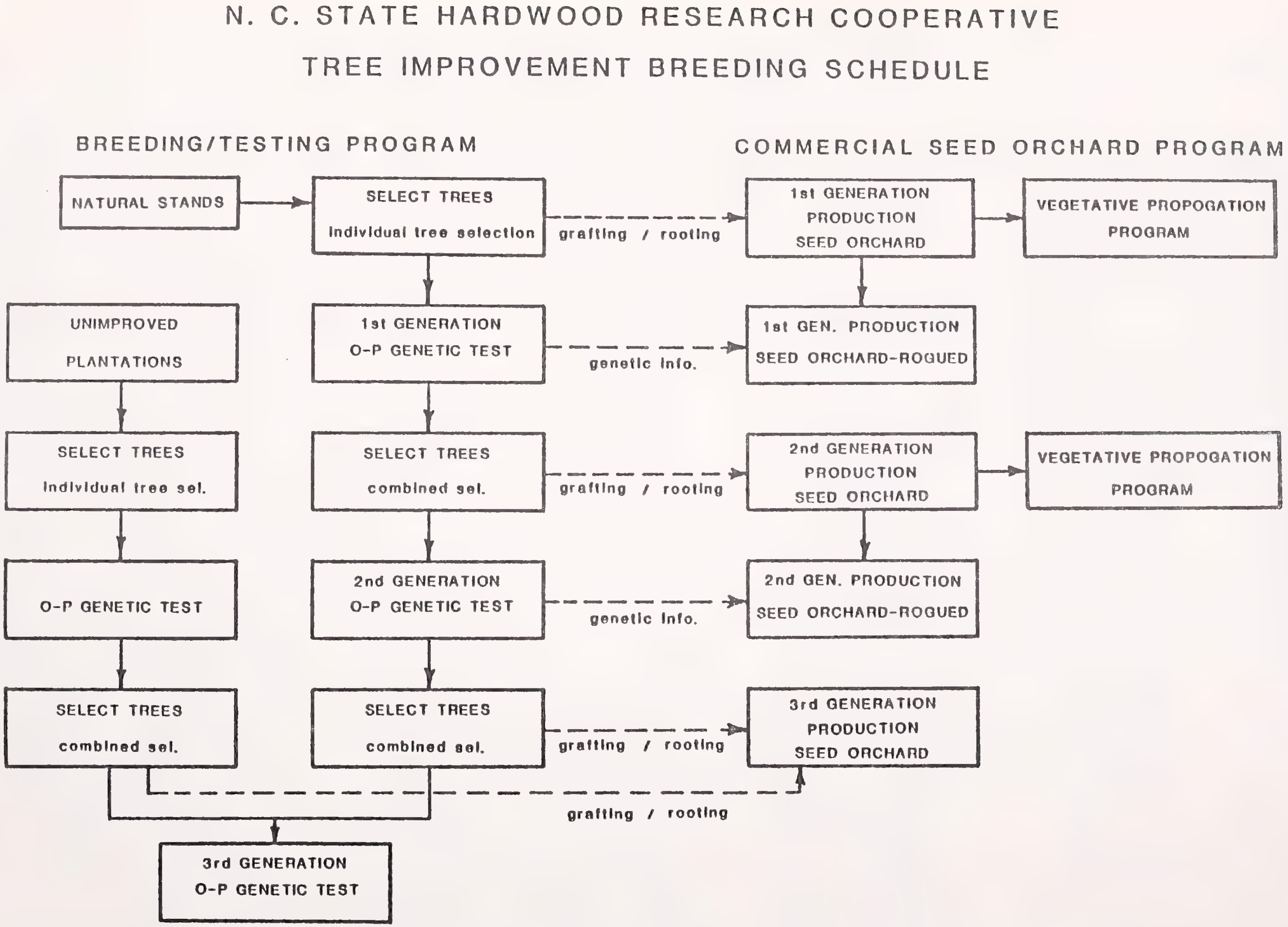

N. C. STATE HARDWOOD RESEARCH COOPERATIVE
TREE IMPROVEMENT BREEDING SCHEDULE
BREEDING/TESTING PROGRAM
COMMERCIAL SEED ORCHARD PROGRAM
NATURAL STANDS
SELECT TREES
Individual tree selection
grafting / rooting
1st GENERATION PRODUCTION SEED ORCHARD
VEGETATIVE PROPOGATION PROGRAM
UNIMPROVED PLANTATIONS
1st GENERATION O-P GENETIC TEST
genetic info.
1st GEN. PRODUCTION SEED ORCHARD-ROGUED
SELECT TREES
Individual tree sel.
SELECT TREES
combined sel.
grafting / rooting
2nd GENERATION PRODUCTION SEED ORCHARD
VEGETATIVE PROPOGATION PROGRAM
O-P GENETIC TEST
2nd GENERATION O-P GENETIC TEST
genetic info.
2nd GEN. PRODUCTION SEED ORCHARD-ROGUED
SELECT TREES
combined sel.
SELECT TREES
combined sel.
grafting / rooting
3rd GENERATION PRODUCTION SEED ORCHARD
grafting / rooting
3rd GENERATION O-P GENETIC TEST

Figure 3.--N. C. State Hardwood Research Cooperative Tree Improvement Breeding Schedule

could become unequal; therefore, the breeding population and individual sublines may need to be supplemented with unrelated individuals to improve the genetic quality of the population. Plans have been made to infuse selections from unimproved plantations that have been shown through progeny testing to be superior genotypes at the third generation. It is important to select and test these supplemental individuals rigorously so that the levels of gain obtained by the third generation will not be diluted when the new selections are added to the breeding population.

The trees chosen from unimproved plantations should be fairly equivalent to selected trees from the third-generation breeding population, even though they have undergone one less cycle of selection, because a stronger selection pressure can be imposed in plantations than in natural stands, leading to a higher initial genetic gain.

Production Phase

The production phase of the improvement program involves the mass production of improved stock and will utilize the very best subset of trees from the breeding population. The improved material can be mass-produced either by seeds from seed orchards or by vegetative propagules. Vegetative propagation has a tremendous potential for the southern hardwoods; however, more research is needed before it is accepted for mass-producing the improved stock.

The cooperating organization's need for improved planting stock will determine when the production phase for that organization begins. Many of the organizations establishing hardwood plantations already have first-generation seed orchards. These seed orchards are being rogued, using genetic information obtained from the open-pollinated genetic tests. For organizations needing improved planting stock and not having a seed orchard, a clonal seed orchard can be established, using superior phenotypes from the open-pollinated genetic tests available in the breeding region or from the best selections from natural stands.

Clonal seed orchards are favored above seedling seed orchards within the Hardwood Cooperative because the design of the first-generation genetic tests is not conducive to conversion to a seed orchard. The second-generation genetic tests are more conducive for converting to seedling seed orchards because the individuals from a family are located in noncontiguous plots instead of row plots. However, the gains from these second-generation seedling seed orchards still would not exceed those of clonal orchards because the clonal orchard could utilize the best individuals from every genetic test in the breeding region, while the seedling seed orchard would be restricted to one test. For the second-generation seed orchard it would be best to utilize the very best individuals from each genetic test in the breeding region.

More improvement could possibly be obtained in advanced generation seed orchards by inserting selected trees from breeding populations from other breeding regions. The feasibility of seed source movement from one region to another will be investigated when breeding populations are established. Progeny from five superior trees from each genetic test within a region will be combined for test establishment in each of the other breeding regions. The design of this trial will be like that of the mother-tree study, comprising six replications of 10-tree row plots.

The design of the clonal seed orchards will be similar to existing hardwood seed orchards, with the size of the orchard depending upon the seed productivity of each species. Dioecious species like green ash pose special problems in production seed orchard design. Generally each planting spot in a seed orchard is both male and female; but for green ash, males and females will have to be positioned for maximum pollination efficiency. To keep seed production per hectare high in the orchard, there will be more female ramets than male ramets. The male clones in the orchard will be restricted to the best four or five clones in the breeding region and will not be rogued from the orchard. There will be many more female clones in the orchard and they will be rogued, using information from the open-pollinated genetic tests.

Accompanying the proposed seed orchard program, an experimental vegetative propagation program will be initiated with anticipation that vegetative propagules will eventually supplement or replace seedlings in reforestation. The best individuals from the breeding population in a given generation will be selected for the vegetative propagation program. Rooted cuttings from these trees will be tested in a number of environments with open-pollinated orchard seedlings of the same clones. These tests will provide information to determine the quality of trees produced from rooted cuttings as compared to seedlings and to better match genotypes to specific environments. By using rooted cuttings instead of seed orchard seedlings for commercial plantations, a greater genetic improvement can be realized because a greater portion of the genetic variance is captured, and the expected increased uniformity of the plantations will make stand management and harvesting easier. The long-term objective will be to replace seedlings and rooted cuttings with unrooted cuttings for plantation establishment.

For all hardwood species, selection of both parents in the breeding population will increase the gains achieved from the seed orchard. The most important reason for selecting both parents and maintaining the option to create control-pollinated families is to minimize inbreeding in the breeding population and production orchard. Inbreeding depression can seriously decrease the realized gain from the improvement program. Limited interest in hardwood breeding programs will dictate that open-pollinated breeding systems be initially used, but the option remains to adopt a control-pollinated breeding scheme after the second generation. A control-pollinated breeding scheme is particularly applicable to an operational planting program utilizing vegetative propagules.

SUMMARY

The area planted to hardwoods is increasing significantly and it is imperative that each additional hectare be planted with the best genetic stock available. The hardwood genetics program at North Carolina State University has undergone a number of changes since its initiation in the early 1960s. The changes have produced groups of selected trees with different levels of improvement. The time has come to integrate the groups into a comprehensive breeding program to provide for continued genetic improvement.

Initially, superior trees were selected and grafted into clone banks and clonal seed orchards with the intention of intermating these trees for the breeding program. It later became evident that genetically superior hardwoods could not be efficiently selected because of stand conditions and the silvics of the hardwood species. An extensive selection system was adopted in which above-average phenotypes were selected and progeny tested, using open-pollinated seed from the selected trees.

The clonal first-generation seed orchards are being rogued, using available genetic test data, and second generation clonal seed orchards are being established by selecting the best trees from the best families in the open-pollinated genetic tests. For the breeding phase, seeds are being collected from a larger set of selected trees from the genetic tests, to create the breeding population for the succeeding generations. Provisions have been made for continued selection of superior trees from unimproved plantations to increase the gene pool of the breeding population for future generations.

For the first generation an open-pollinated system for intermating the selected trees has been adopted, but in later generations control-pollination may be necessary to avoid inbreeding depression and reduce gains from the seed orchards. Along with clonal seed orchards, an experimental vegetative propagation program will be initiated in anticipation that propagules will supplement seedlings in reforestation.

REFERENCES

McKeand, S. E. and W. F. Beineke. 1980. Sublining for half-sib breeding populations of forest trees. Sil. Gen. 29(1):14-17.

Sweet, G. B. and L. Wells. 1974. Comparison of the growth of vegetative propagules and seedlings of Pinus radiata. New Zealand Jour. For. Sci. 4(2):399-409.

ECONOMIC BENEFITS OF AN AGGRESSIVE BREEDING PROGRAM

S. E. McKeand and R. J. Weir[1]

Abstract: Before any new methods are used to speed up the breeding cycle in a tree improvement program, the economic benefits of the techniques need to be evaluated. New technologies must yield a suitable rate of return for the money invested, if they are to be utilized in applied programs. Many new methods are available which will speed up the breeding cycle: out-of-phase dormancy, indoor potted breeding facilities, gibberellin applications, containerized planting stock for genetic tests, etc. Some of the methods require substantial investments and may not be economical. Other methods require very little additional time and money and may result in high returns on investment.

A present value analysis was done to determine the economic benefits of shortening the breeding cycle of loblolly pine (*Pinus taeda* L.) by 1 to 6 years in the southeastern United States. Depending upon various conditions such as stumpage values, desired rate of return, and the number of acres regenerated with the improved planting stock, the investment in aggressive breeding programs will be very profitable in most tree improvement programs.

INTRODUCTION

Many new methods to accelerate the breeding cycle for loblolly pine (*Pinus taeda* L.) have been developed in recent years. Out-of-phase dormancy (Greenwood 1978), indoor potted breeding facilities (Greenwood *et al*. 1979), water stress and gibberellin applications (Greenwood 1981), outdoor potted breeding facilities (Anonymous 1983), and proper site selection, irrigation, and fertilization regimes for conventional field established orchards (Jett 1983) have all shown positive results in speeding the reproduction cycle in loblolly pine.

Before any of these new methods are used in a tree improvement program, the economic benefits of the techniques need to be evaluated. If new technologies do not yield a suitable rate of return for the money invested, then there is no justification for utilizing them. This paper will outline the biological and economic benefits which can be gained from accelerated breeding schedules for loblolly pine.

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The cycle from the beginning to end of a tree improvement generation is long and complex. The steps involve selection, breeding, testing, production of commercial quantities of seed, and, finally, the crop production through rotation. This complete cycle normally requires 50-60 years to complete for loblolly pine. If any portion of it can be shortened without adversely affecting the quality and yield of the crop at rotation age, much more economic gain will be realized. We will limit the discussion to shortening only the breeding phase of the tree improvement cycle. The only effect that a shorter breeding cycle has is to get the genetic gain into production at an earlier date. The amount of gain is not affected.

In the North Carolina State University-Industry Cooperative Tree Improvement Program, the goal has been established to complete the second generation interval of breeding, testing, and selection in 20 years. The breeding phase is expected to require 12 years to complete and selection will occur in 8 year-old genetic tests (Anonymous 1982). With intensive accelerated breeding methods such as out-of-phase dormancy and an indoor potted breeding facility, the breeding phase might be shortened to 6 years rather than 12 years (Greenwood et al. 1979). The effect of this on the amount of genetic gain per year is illustrated in Figure 1. If 15% genetic gain is achieved in 20 years, 0.75% gain per year results. If the interval is reduced by 6, 1.07% gain per year or 43% more benefit is realized. To achieve this extra benefit, additional costs will be involved. Therefore, the objective of our tree improvement activities is to optimize the amount of genetic gain per unit time so as to maximize the rate of return for the investment in tree breeding.

METHODS

A present value analysis was done to show the value of saving time in a tree improvement cycle. Two successive cycles of improvement were evaluated with the biological assumptions being:

- Genetic gain equal to 15% of value per generation.
- Base growth rate for land is 1.5 cords/acre/year.
- Twelve years after grafting are required to complete breeding without using flower stimulation methods.
- Selections from progeny tests will be made at age 8.
- Seed orchards begin full production at age 12.
- Rotation length equals 25 years.

The biological benefits of speeding up the breeding activities are shown in Figure 2. If two consecutive breeding cycles are shortened by six years, an extra 15% value per acre, measured as 5.6 and 6.5 cords per acre, respectively, will be harvested for 6 and 12 years sooner from the first and second generations of improvement, respectively.

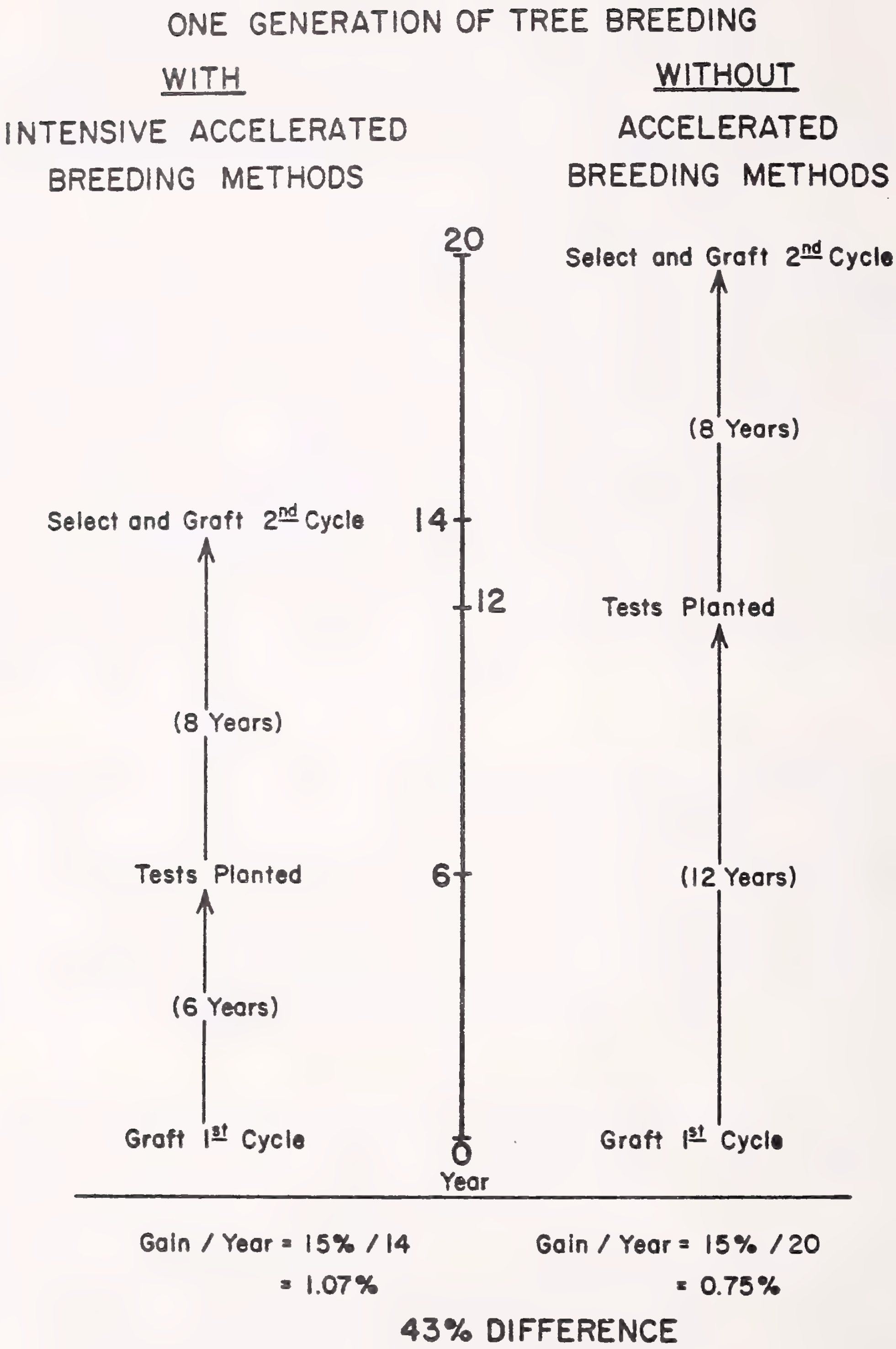

Figure 1.--One Generation of Tree Breeding With and Without Intensive Accelerated Breeding Methods.

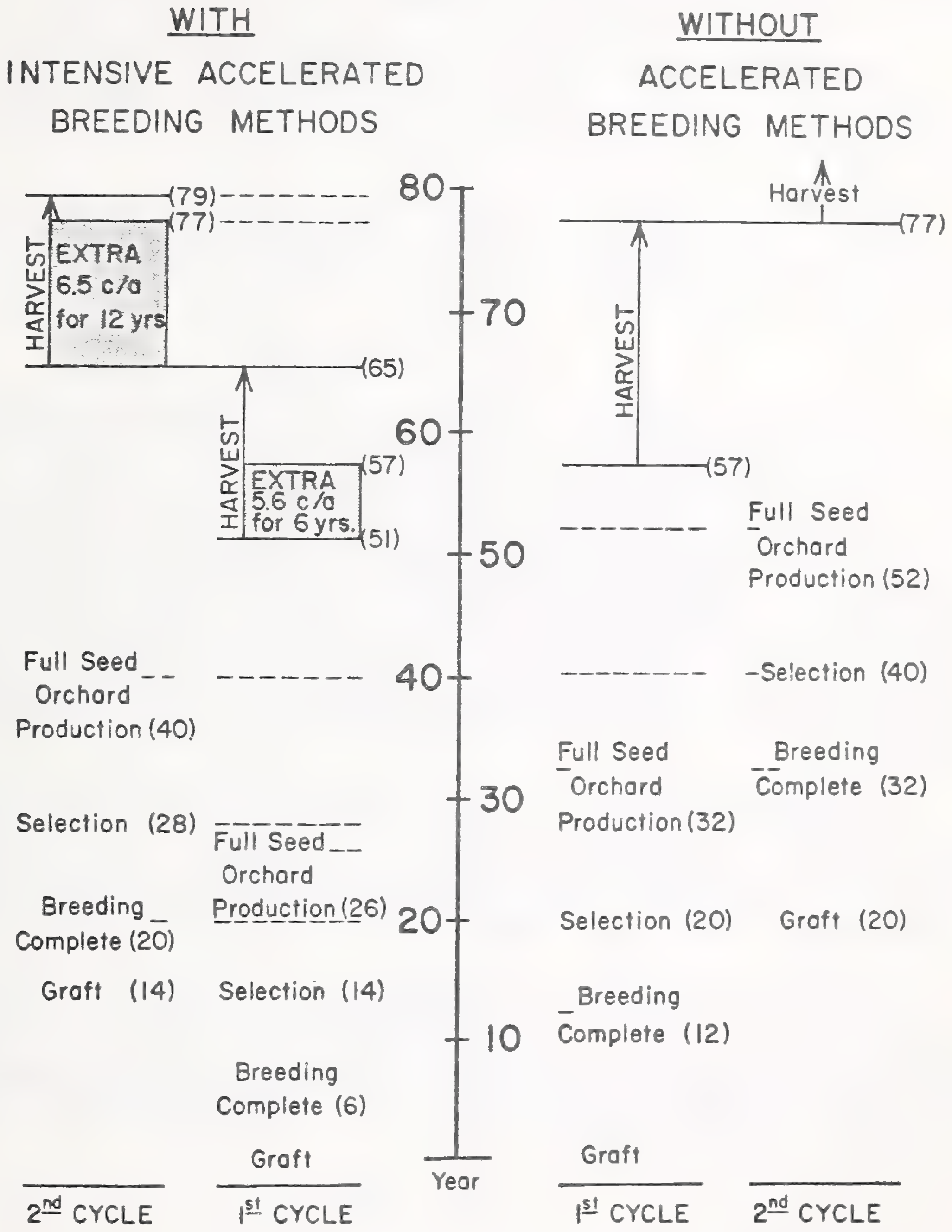

Figure 2.--Result of Reducing the Breeding Cycle from 12 to 6 years for 2 generations of improvement.

The economic benefits of the time savings were determined by discounting the future value of the increased harvest to today's dollars. Stumpage prices were increased at a rate of 2% per year above inflation. This has been a trend in the South for several years and is expected to continue as demand for southern pine fiber increases (Anonymous 1982b, Clephane 1982).

The analyses were done for stumpage values of $15 and $25 per cord, with rates of return of 6%, 8%, 10%, and 12%. The number of years which could be saved varied from one to six years. The present values were calculated for a 10,000 acre per year regeneration program.

No attempt was made to include cost figures in the economic analysis for the various treatments used in accelerated breeding programs. Most of the methods are relatively new and little information regarding the costs of treatments is available.

RESULTS AND DISCUSSION

The values presented in Table 1 indicate that investing in accelerated breeding methods will be very profitable in most cases. Saving as little as one year in the breeding cycle is worth a great deal of money. At an 8% discount rate and $15 per cord stumpage price, the present value of the time savings would be over $60,000 for a 10,000 acre per year regeneration program. For a larger program of 30,000 acres per year regeneration and $15 per cord stumpage, if 6 years could be eliminated from the breeding cycle, the present value would be $2,251,500 (i.e. 3 times the Table 1 value for 10,000 acre program) at an 8% discount rate. A variety of time savings, stumpage prices, and discount rates can be evaluated from Table 1. The analysis is quite sensitive to the discount rate used, because of the long time period for the investment.

Many low cost methods such as gibberellin applications for female stimulation, wire girdling for pollen stimulation, or growing seedlings in containers in a greenhouse are all workable methods to reduce the breeding cycle from 1 to 3 years. Very little added expense would be incurred if these methods were used, but very large economic benefits would result.

There is no set answer as to whether or not certain investments are justified to accelerate a breeding program. The analyses which were presented are simplified. No consideration was given to important factors such as depreciation of equipment or structures, operating costs, or taxes. However, it should be apparent that investing in an aggressive breeding program will be profitable in most situations.

Table 1.--Present Value for Saving 1-6 Years per Tree Improvement Cycle for 2 Cycles for Regenerating 10,000 Acres per Year.[1]

Years Saved	Today's Stumpage ($/Cord)	Desired Rate of Return[2]			
		12%	10%	8%	6%
1	15	$ 6,200	$ 18,800	$ 60,300	$ 204,200
	25	10,300	31,300	100,500	340,300
2	15	13,100	39,600	125,800	420,800
	25	21,800	66,000	209,700	701,300
3	15	20,900	62,700	197,100	651,000
	25	34,800	104,500	328,500	1,085,000
4	15	29,800	88,300	274,400	894,800
	25	49,700	147,200	457,300	1,491,300
5	15	39,800	116,800	358,600	1,153,600
	25	66,300	194,700	597,700	1,922,700
6	15	51,200	148,600	450,300	1,428,500
	25	85,300	247,700	750,500	2,380,800

[1] For different number of acres to be regenerated, multiply the table value by the appropriate factor (ie. 2 x for 20,000 acres) to obtain the proper present value.

[2] Real interest rate, above inflation.

LITERATURE CITED

Anonymous. 1982a. 26th Annual Report. N. C. State University-Industry Cooperative Tree Improvement Program. 72 p.

Anonymous. 1982b. An analysis of the timber situation in the United States 1952-2030. USDA For. Serv. Rept. No. 23. 499 p.

Anonymous. 1983. 27th Annual Report. N. C. State University-Industry Cooperative Tree Improvement Program. 66 p.

Clephane, T. P. 1982. Outlook for timber supply demand through 1990. In: Workshop Proceedings. Financing Forestry Investments: Attracting private capital to timber and timberland. p. 18-52.

Greenwood, M. S. 1978. Flowering induced on young loblolly pine grafts by out-of-phase dormancy. Science 201:443-444.

Greenwood, M. S. 1981. Reproductive development in loblolly pine. II. The effect of age, gibberellin plus water stress and out-of-phase dormancy on long shoot growth behavior. Amer. J. Bot. 68:1184-1190.

Greenwood, M. S., C. H. O'Gwynn, and P. G. Wallace. 1979. Management of an indoor, potted loblolly pine breeding orchard. Proc. 15th South. For. Tree Impr. Conf. p. 94-98.

Jett, J. B. 1983. The impact of irrigation and supplemental nitrogen fertilization on the development of a young loblolly pine seed orchard. Ph.D. Thesis, N. C. State Univ. 38 p.

Low Level Inbreeding Effects on Germination, Survival, and Early Height Growth of Slash Pine

P. A. Layton and R. E. Goddard[1]

ABSTRACT

Four progeny tests containing back, half-sib, and out crosses of slash pine were established near Lake Butler, Florida; two each in 1980 and in 1981. Height and survival were measured in 1982 and 1983. Crossing types were not significantly different for these traits in the four tests. For the three tests in which all cross types were planted, average survivals for back, half-sib, and out crosses were 86%, 83%, and 99%, respectively. Average heights for back, half-sib, and out crosses were 57, 59, and 63 cm in 1982 and 132, 137, and 150 cm in 1983, respectively. Height and survival for the crossing types are inversely related to the inbreeding coefficient. Seed germination of the same families was tested in a greenhouse. Percent germination at nineteen days was 94, 78, and 94 percent for back, half-sib, and out crosses, respectively. Means were not significantly different.

Additional Keywords: *Pinus elliottii* var. *elliottii*, inbreeding depression.

Previous inbreeding studies of forest trees have considered mainly self-pollination. Results show inbreeding adversely affected seed yield, germination, seedling morphology, and tree vigor and growth (Table 1) and concluded that inbreeding should be avoided if at all possible. However, small effective population size precludes avoidance of inbreeding. Van Buijtenen (1975) suggests separation of breeding and production populations with the breeding population subsetted into small groups where inbreeding is allowable. The production population would contain one selection from each group. Inbreeding and inbreeding depression would only affect the breeding population; the production population being totally out crossed except for an estimated 2.5% selfing (Squillace and Goddard, 1982). Within breeding groups the average co-ancestry after 10 generations is predicted to be less than 0.425 for two mating designs (Layton 1978).

What then are the effects of low levels of inbreeding? Squillace and Kraus (1962) estimated that with an increase of 0.1 in the inbreeding coefficient, slash pine (*Pinus elliottii* var. *elliottii* Englem.) had five fewer sound seeds per cone, an 8% decrease in germination, a 7% decrease in rate of germination, and a 4% decrease in seedling height. Their study provided some insight of the effect of low levels of inbreeding; however, as slash pine

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Table 1.--Studies of various conifer species presenting evidence of inbreeding depression.

Species	Common Name	Study	Inbreed Cross Used
Pinus elliottii var. elliottii Engelm.	Slash pine	Squillace and Kraus 1962	Self Back Full-sib
		Snyder 1968, 1972	Self
		Gansel 1971	Self Back Half-sib Full-sib
Pinus taeda L.	Loblolly pine	Franklin 1969	Self
Pinus monticola Dougl.	Western white pine	Barnes 1964	Self
		Bingham 1973	Self
Picea abies	Norway Spruce	Andersson et al. 1974	Self
Pinus banksiana Lamb.	Jack Pine	Fowler 1964	Self
Pinus strobus L.	Eastern white pine	Fowler 1964	Self
Pseudotsuga menziesii (Mirb.) Franco	Douglas-fir	Orr-Ewing 1954	Self
		Sorensen and Miles 1982	Self
Pinus ponderosa Dougl. ex. Laws.	Ponderosa pine	Sorensen and Miles 1982	Self
Sequoia sempervirens (D. Don) Endl.	Redwood	Libby et al. 1981	Self

breeding has progressed, interest in the effects of inbreeding has increased. Further study is needed to increase the knowledge of these effects over time, and over a wide range of genotypes.

MATERIALS AND METHODS

In 1975, the University of Florida Cooperative Forest Genetics Research Program initiated a study to examine effects of low level inbreeding on slash pine growth. The study was designed to include back crosses, half-sib crosses, out crosses, and selfs, but the self-pollinations were not completed. The inbreeding coefficients for the progeny of these crosses, assuming no prior inbreeding, are 0.0, 0.125, and 0.25 for out, half-sib, and back crosses, respectively (Squillace and Kraus 1962). Control pollinations were made at the Owens-Illinois, Inc. seed orchard in White Springs, Florida. The orchard contained mostly second generation selections of slash pine from open-pollinated progeny tests with two to five different half-sib clones of 11 families available for crossing. In 1980 two tests (3A and 3B) were planted near Lake Palestine in Baker County, Florida on a cleared and bedded site. Ten replications of six families of each of the three cross types (back, half-sib, and out) were planted in four-tree row plots in each test.

In 1981, two tests were established nearby in Union County, Florida on a bedded but much wetter site. Test 4A contained only half-sib and out crosses, while the main test, 4B, had all three cross types. Five-tree row plots were replicated ten times in each test.

Comparisons among tests were not possible because only one cross was common to all four tests while two crosses were common to three of the tests. Sixty-seven different crosses were represented in all tests (Table 2).

Plot means were obtained for survival and height from measurements in 1982 and 1983. Variances for each test in each year were analyzed using the Statistical Analysis System (Helwig and Council 1979). Factors considered in the model were cross type (back, half-sib, and out), families within cross type, replications, replication by cross type interaction, and experimental error (Table 3).

In 1982 seed from 47 of the crosses (8 out, 36 half-sib, and 3 back crosses) were evaluated for germination. From 50 to 100 seeds per family were germinated in flats of vermiculite in a greenhouse. Seeds were soaked in water 24 hours and placed in flats. The number of seed available and the number of germinated seed at approximately two-day intervals from day eight to day nineteen was recorded.

Percent germination after 19 days was computed. Results were analyzed using analysis of variance for a completely randomized design. Germination rates were calculated by the formula:

$$\text{Germination Rate} = \frac{\text{Germination count at 10 days}}{\text{Germination count at 19 days}} \times 100.$$

These data were analyzed in the same manner as percent germination.

Table 2. Families present in four slash pine progeny tests by crossing type.

	Test			
Back	3A	3B	4A	4B
1901 x 249-55				X
1902 x 249-55	X	X		X
1903 x 249-55				X
0301 x 17-57	X			
0601 x 84-57	X			
0804 x 106-56				
0805 x 106-56	X	X		
3701 x 11-57	X	X		
0201 x 262-55	X	X		
0202 x 262-55	X			
3601 x 248-56				X
0307 x 17-57	X			
3602 x 248-56				X
Out				
0603 x 0402				
0703 x 0201	X	X		
0703 x 0301	X	X		
0703 x 0402	X			
0703 x 0603	X	X		
0703 x 0804	X	X		
0703 x 1902	X	X		
0703 x 3701	X			
0802 x 0301	X			
0804 x 0305	X			
0401 x 0608			X	X
0402 x 0608			X	X
0403 x 0608				X
0702 x 0306			X	X
0802 x 1301			X	X
0802 x 3602			X	X
0804 x 3602			X	X
0807 x 0702			X	X
0807 x 1301			X	X
0807 x 3602			X	X
0809 x 1301			X	X
0809 x 3602			X	X
3701 x 3607			X	X
3702 x 3602			X	X

	Test			
Half sib	3A	3B	4A	4B
0602 x 0603	X		X	X
0607 x 0603	X			
0610 x 0603	X	X		
0802 x 0804	X	X		
0802 x 0805	X	X	X	X
0804 x 0805	X	X		
0807 x 0804	X			
0302 x 0307			X	
0303 x 0301				X
0303 x 0305				X
0304 x 0301				X
0304 x 0305				X
0401 x 0402				X
0402 x 0401			X	X
0403 x 0401			X	X
0602 x 0608				X
0603 x 0604				X
0603 x 0608			X	X
0606 x 0603				X
0610 x 0604				X
0611 x 0608				X
0703 x 0702				X
0802 x 0801			X	X
0804 x 0801			X	X
1903 x 1901			X	X
1903 x 1902			X	X
2001 x 2003				X
2004 x 2003				X
3601 x 3602			X	X
0303 x 0307				X

Table 3.--Expected mean squares and degrees of freedom for the model used to analyze height and survival.

Source	df	Expected Mean Squares
Total	179	
Cross	2	$\alpha^2_e + 6\alpha^2_{r \times c} + 10\alpha^2_{f(c)} + 60\alpha^2_c$
Family (Cross)	12	$\alpha^2_e + 6\alpha^2_{r \times c} + 10\alpha^2_{f(c)}$
Replication	9	$\alpha^2_e + 18\alpha^2_r$
Replication x Cross	18	$\alpha^2_e + 6\alpha^2_{r \times c}$
Error	138	α^2_e

RESULTS AND DISCUSSION

Survival

Survival in each of the four tests was over 80%. In tests 3A and 3B initial survival values were 88.6% and 88%, respectively. Tests 4A and 4B, planted one year later, averaged 81.6% and 81.2%, respectively. There were no significant differences in survival between back, half-sib, and out crosses. Outcrosses had better survival than the inbreed crosses in three of the tests (Table 4). The differences in survival between out crosses and inbred crosses

Table 4.--Survival by crossing type for four slash pine progeny tests planted in Florida, 1980 and 1981.

Test	Age (yrs)	Type of Cross		
		Back	Half-sib	Out
3A	2	86.4	86.7	92.3
	3	86.0	85.4	91.7
3B	2	83.0	90.0	91.0
	3	83.0	90.0	91.0
4A	1	-	82.0	80.4
	2	-	81.1	80.4
4B	1	82.2	79.3	82.8
	2	81.8	78.8	82.3

was below eight percentage points. There were significant differences for families within cross types in Test 4A and 4B for both first and second year survival measurements. Site conditions, especially the presence of standing water, may have influenced survival of tests 4A and 4B.

Height

Heights were not significantly different among cross types. Test 4B had significant differences for families within crosses at age one, but there were no significant differences in this factor at age two. Height in tests 4A and 4B was greater at ages one and two than height at age two and three in tests 3A and 3B (Table 5). Differences reflect site quality. On the average out crosses were taller than half-sib and back crosses for both ages in tests 3A and 3B. Height differences between out crosses and inbred crosses increased from age two to three in both of these tests (Table 5). Test 4A followed the same pattern. Half-sib crosses averaged 0.3 cm taller than back crosses at age one in test 4B, but at age two were 9.4 cm shorter, a 5.5% decrease in height when compared to the out-cross mean height.

Table 5.--Mean height by crossing type for four slash pine progeny tests planted in Florida, 1980 and 1981.

Test	Age (yrs)	Control (cm)	Back Cross (cm)	Deviation from Out Cross (%)	Half-sib Cross (cm)	Deviation from Out Cross (%)	Out Cross (cm)
3A	2	54.2	51.6	-10.8	52.5	-9.7	57.8
	3	110.7	101.3	-16.8	107.8	-11.5	121.8
3B	2	61.9	59.1	-11.2	60.2	-9.4	66.5
	3	146.4	137.3	-13.6	143.3	-9.8	158.9
4A	1	62.6	-	-	61.7	-3.1	63.6
	2	166.6	-	-	162.5	-4.9	171.0
4B	1	64.0	61.3	-4.7	64.7	+0.005	64.3
	2	165.3	157.5	-7.5	160.8	-5.5	170.2

The general trend for heights was for out crosses to be tallest, followed by half-sib and back crosses (Figure 1). Although more variable, means by individual parent have similar height trends (Table 6). In a few individual cases, however, no inbreeding depression was apparent. This may be due to experimental error, but suggests that some genotypes contain few recessive deleterious genes.

Germination

Percent germination and germination rates were not significantly different between cross types. Average percent germination was 93.9%, 77.9%, and 91.3% for back, half-sib, and out crosses, respectively. Mean germination rate for back crosses was 98.5%, followed by out crosses, 83.8%, and half-sib crosses, 78.7%, however, estimates of back cross germination are based on only three crosses. Out crosses had better percent germination and germination rates than half-sib crosses.

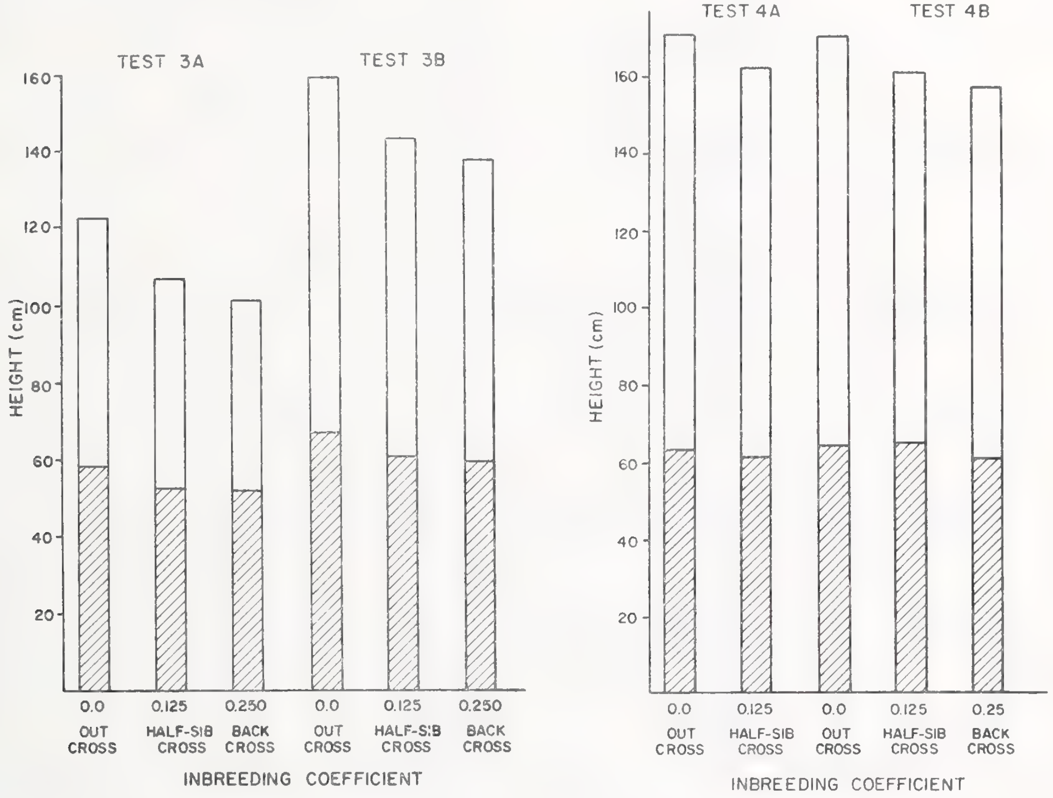

Figure 1. Mean heights by crossing type for four slash pine progeny tests planted in Florida, 1980 and 1981. Shaded areas are heights at ages 2 and 1 and clear areas are heights at ages 3 and 2 for the 1980 and 1981 plantings, respectively.

SUMMARY AND CONCLUSIONS

No significant differences occurred in early height, survival, or germination of out, half-sib, and back crosses of slash pine. Height and survival were inversely related to the inbreeding coefficient. These data agree with other studies of inbreeding depression.

The material available for the several plantings was insufficient for comparison among tests, therefore, data from each planting must be interpreted independently. The trend of lower height growth with increase in inbreeding coefficient was similar in all plantings, and to date, the suspected inbreeding depression seems to be increasing with age of the material planted.

Table 6.--Mean progeny heights when parents are crossed as back, half-sib, or out crosses for two slash pine tests planted in Florida, in 1980 and 1981.

Test	Age	Parent	Mean Height		
	(yrs)		Back Cross	Half-sib Cross	Out Cross
			(cm)		
3A	3	0201	89	-	127
		0301	135	-	103
		0601	138	118	-
		0603		121	114
		0802		114	103
		0804	88	102	111
		0805	90	123	-
		1902	94	-	137
		3701	101	-	83
		Test Average	101	108	122
4B	2	0301	-	159	181
		0401	-	178	200
		0402	-	164	181
		0403	-	165	204
		0608	-	155	187
		0702	-	97	172
		0802	-	156	176
		0804	-	79	174
		1901	173	162	-
		1903	132	162	-
		3601	170	209	-
		3602	167	209	164
		Test Average	157	161	170

LITERATURE CITED

Andersson, E., R. Jansson, and D. Lindgren. 1974. Some results from second generation crossings involving inbreeding in Norway spruce (*Picea abies*). Silvae Genet. 23:34-43.

Barnes, B. V. 1964. Self-and cross-pollination of western white pine: A comparison of height growth of progeny. USDA For. Serv. Res. Note INT-22. 3 pp.

Bingham, R. T. 1973. Possibilities for improvement of western white pine by inbreeding. USDA For. Serv. Res. Paper INT-144. 18 pp.

Fowler, D. P. 1964. Effects of inbreeding in red pine, *Pinus resinosa* Ait. IV. Comparison with other northeastern *Pinus* species. Silvae Genet. 14:76-81.

Franklin, E. C. 1969. Inbreeding depression in metrical traits of loblolly pine (*Pinus taeda* L.) as a result of self-pollination. Technical Report 40. N.C. State Univ. Coop. Prog., Raleigh. 19 pp.

Helwig, J. T. and K. A. Council. 1979. SAS user's guide. 1979 edition. SAS Institute, Inc., Cary, N.C. 494 pp.

Gansel, C. R. 1971. Effects of several levels of inbreeding on growth and oleoresin yield in slash pine. Eleventh South. For. Tree Improv. Conf. Proc. pp. 174-176.

Layton, P. A. 1978. Comparison of two advanced generation mating designs for loblolly pine (*Pinus taeda* L.). Master's Thesis, Texas A & M Univ. College Station. 47 pp.

Libby, W. J., B. G. McCutchan, and C. I. Millar. 1980. Inbreeding depression in selfs of redwood. Silvae Genet. 30:15-25.

Orr-Ewing, A. L. 1954. Inbreeding experiments with the Douglas-fir. For. Chron. 30:7-20.

Snyder, E. B. 1968. Seed yield and nursery performance of self-pollinated slash pines. For. Sci. 14:68-74.

Snyder, E. B. 1972. Five year performance of self-pollinated slash pines. For. Sci. 18:246.

Sorensen, F. C. and R. S. Miles. 1982. Inbreeding depression in height, height growth, and survival of Douglas-fir, ponderosa pine, and noble fir to 10 years of age. For. Sci. 28:283-292.

Squillace, A. E. and J. F. Kraus. 1962. Effects on inbreeding on seed yield, germination, rate of germination, and seedling growth in slash pine. For. Genet. Wkshp. Proc., Macon, Georgia. pp. 59-63.

Squillace, A. E. and R. E. Goddard. 1982. Selfing in clonal seed orchards of slash pine. For. Sci. 28:71-78.

van Buijtenen, J. P. 1975. Advanced generation breeding. Thirteenth South. For. Tree Improv. Conf. Proc. pp. 63-72.

THE QUESTION OF GENETIC MANAGEMENT OF MINOR OR UNDOMESTICATED SPECIES--AN OUTSIDER'S REACTION

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Abstract.--Many of the tree species in the Southeast are not being subjected to breeding work, either because other species are preferred, or because although important wood sources they are not favoured for intensive cultivation. Even with minor species for which orchard programs exist the availability of seed from the orchards can actually provide a disincentive to the provision of a broad genetic base in a form that is readily utilised and which may ultimately be needed.

Considerations are examined for the genetic management of such species in preparedness for future changes in the situation. While there is no apparent problem with overall gene conservation, there are difficulties in securing some soundly-based genetic improvement at minimal outlays. Pilot-scale cultivation of the species could provide the opportunity for judicious improvement measures, largely incidental to the cultivation. A key factor will be establishing, where possible, plantations that are broadly based genetically.

STATUS OF SPECIES

There are many tree species in the Southeast which are not being genetically improved because they are not favoured propositions for regeneration and intensive management. Reasons for this include:

1. inherently slow growth rates and/or poor tree form, at least in comparison with the preferred species,
2. no special premium on wood values,
3. difficulties of artificial regeneration involving:
    - seed collection
    - seed handling and storage
    - nursery culture and plantation establishment
    - slow initial growth and inflated weeding costs
4. site sensitivity, either requiring very good land, or leading to uneven and often poor growth,

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5. possibly, difficulties arising with growing the species in pure stands.

Even if seed orchards exist the species are only being improved inasmuch as they are being regenerated artificially. Nevertheless, such species are of interest, over and above any consideration of straightout conservation for one or more of the following reasons.

1. Many of them occupy large areas of land, which are likely to remain in such species for a long time.

2. Some are potential substitutes for loblolly and slash pines, these being basically the remaining or "minor" pines species. As such they could rise in importance if loblolly or slash pine should fall into disfavour, through pressures to plant more difficult sites, through increased concentrations accentuating known disease hazards, or through the emergence of new factors.

3. Others, namely the hardwoods, are largely complementary to the pines in their utilization characteristics. They are sources of short-fibred pulp and potentially of sawn timber. However, only black walnut, black cherry and perhaps green ash fall into the high-value specialty bracket, while at the other end of the scale tulip poplar could at least partially substitute for pines

Then there are some special cases like Fraser fir, which provides Christmas trees.

CONSIDERATIONS FOR GENETIC MANAGEMENT

Since those species are of interest we must be concerned with their genetic management in terms of:

- preservation of basic gene resources,
- achieving some measure of actual genetic improvement, or at least heading off crop deterioration.

The gene resource question is not a problem in itself, since the occurrence of such species, often in numerous small demes but well scattered over large areas, would seem to be a highly favourable situation for preserving the total gene resources (cf Brown, 1978). Moreover, it is understood that the U.S. Forest Service is currently examining this question. That the demes should often be decidedly inbred should not matter in relation to preservation of alleles over large regions, while the 'soft' (density-dependent) selection situations that can prevail under conditions of natural regeneration mean that homozygotes can be selectively eliminated in favour of balanced heterozygotes at little cost in terms of final crop fitness. Nevertheless, natural stands, through the inbreeding effects and through the tendency to give relatively low field heritabilities, do not provide such readily usable gene resources as broadly-based plantations would.

Genetic improvement is much more of a problem. To be practised at all it requires reasonably intensive management of the stands (compared with laissez-faire exploitation) and an important (if not necessarily essential) component of such management is artificial regeneration. While this approach would normally be the most profitable for those who acquire land as a basis for sustained yield wood production (Franklin, 1980), many of the actual land owners do not have the financial resources to embark on intensive management, and if they did they would be likely to establish with P. taeda. Artificial regeneration of the hardwood species just for pulpwood crops would in most cases appear very unattractive economically. Establishment for these species for producing high quality logs may have some attractions, but the generally modest inherent value of the timber or the site requirements for producing quality logs would tend to limit the scale on which this might be done.

In any case, if artificial regeneration is to be done by planting, there will be a heavy outlay and a high proportion of the genotypes planted will need to be fully fit. Exceptions, though, would be species that are readily propoagated as cuttings. In these, a certain proportion of unsatisfactory genotypes in seedlots could be eliminated quite painlessly during the early stages of selecting genotypes for vegetative propagation. Direct seeding could save costs (although it might still require good site preparation) and can allow for a greater wastage of genotypes, but will require considerably more seed. Its feasibility as an option is not generally established, but it is potentially attractive for low-effort genetic management on account of the scope it allows for natural selection.

These factors all argue against a heavy commitment to genetic improvement of such species. Nevertheless, it seems prudent to have their genetic management in hand, so that if and when it is desired to cultivate the species there should be satisfactory seed sources available which would represent the genetic improvement that could be obtained, with minimum outlay, over a period of time.

For any particular species (other than the major ones that are already subject to intensive breeding programmes), it would appear to be a question of:

> Does one have the management of genetic material in hand, with a low outlay on the actual genetic improvement work, so as to provide for:
>
> 1. shakeout of neighbourhood inbreeding effects,
>
> 2. reasonably effective selection in the field,
>
> 3. pursuing continued genetic improvement on a satisfactory genetic base?

This question can be resolved into a further series of questions:

1. Are there seed orchards?

2. If so,

    a. are the orchards likely to represent appreciable genetic improvement? In other words, was there a worthwhile heritability under the conditions of initial field selection?

    b. do the seed orchards represent a worthwhile genetic base for going further? This requires, preferably, that the seed orchards should represent some genetic improvement in themselves but, much more important, that the orchard clones available within a safe breeding region should be numerous, say $\geq$ 200, and unrelated.

    c. if there are sufficient clones, are there progeny test plantings which would allow effective second-generation selection? It would seem important that such plantings should give good individual heritabilities (to avoid the need for elaborate selection procedures), and that the layout should not be conducive to undue inbreeding, since such plantings would effectively be seedling seed orchards.

3. If there are no orchards, or if neither the orchards nor the progeny tests represent a satisfactory base for long-term genetic management, are there broadly-based plantations which would meet the basic requirements? These would have to be based on large numbers of unrelated parents, and have had a history that would be expected to give worthwhile field heritabilities which would make mass-selection reasonably efficient.

A POTENTIAL PROBLEM

From this analysis I can see one particular strategy problem brewing, a problem that would be more psychological than techincal in its basis. It concerns the species for which seed orchards have been established with limited numbers of intensively selected clones, and are now producing seed far in excess of current planting requirements. Several of the 'minor' pine species clearly belong in this category (Anon., 1976).

In hindsight, it seems that seed orchards, while often an appropriate first step for genetic improvement, may be appropriate only when a firm and high-level commitment to this improvement can be sustained. Establishing seed orchards without intensive large-scale follow-up may achieve very little. Indeed I suggest it has some positive dangers. The presence of orchards, whose production is not really being used, must serve as a powerful disincentive to establishing plantations with broadly-based seedlots. With some such species current plantings are essentially on an experimental scale, and even if orchard seed is not used it can be all too easy to obtain the requisite seed just from a few neighbouring trees.

CONCLUDING REMARKS

I use the term "genetic management" partly to avoid any notion of a heavy investment in breeding work, and partly with a view to being in a state of preparedness for any future situation in which there could be an abrupt increase in the cultivation of the species in question.

Very important could be the genetic improvement measures that can be carried out incidental to any cultivation of the species that is already being practised, or to any pilot work that is being done on the cultivation. The appropriate scale of the pilot operations may in itself be arbitrary, in which case the scale could well be fixed to satisfy considerations of genetic management. If the seed can be collected in the course of setting up genecological studies that remain to be done, so much the better. In any case the best prospects seem to lie in bringing together a broad genetic base, and creating a reasonable field heritability, and allowing natural and silvicultural selection to operate. Present economic conditions and the lack of day-to-day urgency must be a brake on immediate action. So will the rather fluid state of the respective roles of government and private agencies. I would urge, though that responsibilities be decided now and that firm targets be set for, say, the next five years.

Much will depend on biological constraints, such as the seed production and other propagation characteristics of particular species, and on the sort of field heritabilities that can be expected. The prospective payoffs, modest though they might seem, must be weighed against the possibility of dysgenic effects in the absence of any positive action.

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REFERENCES

Anon. 1976. North Carolina State University - Industry Cooperative Tree Improvement Program Twentieth Annual Report.

Brown, A. H. D. 1978. Isozymes, plant populations, genetic structure and genetic conservation. Theoretical and Applied Genetics 52:145-57.

Franklin, E. C. 1980. An expanded concept of the role of forest industry in private and industrial forestry. Tappi 63(12):99-101.

CROWN-QUALITY ASSESSMENT AND THE RELATIVE ECONOMIC IMPORTANCE OF GROWTH AND CROWN CHARACTERS IN MATURE LOBLOLLY PINE

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ABSTRACT

The size and number of knots in 2.6-meter loblolly pine (Pinus taeda L.) veneer bolts was significantly negatively related to the dollar value of veneer from those bolts in a multiple-regression model which also included bolt size, taper and sweep. However, when this model was used to predict whole-tree dollar value, the impact of quality-related improvements in stem knottiness on dollar value of a tree was insignificant in comparison to the impact of tree size. Individual branching traits and combinations of branching traits could be measured more repeatably on standing trees than could a subjective crown-score, but crown and branch traits, like stem knot traits, were either unimportant to tree value or were important only as a function of their relationships to tree size. Increasing the relative value of high-grade veneer shifted the regression coefficients for the crown and branch traits in a direction suggesting a greater influence of stem quality on tree value. The relative importance of crown and branch traits to tree dollar value for other product outcomes should be evaluated, and economic and genetic information combined in a multi-trait index, before the final decision is made to include or discard such traits in future rounds of selection.

INTRODUCTION

Lessons learned during the first generation of loblolly pine (Pinus taeda L.) improvement provide a means by which time and resources can be allocated more efficiently in advanced generations. One aspect of first-generation improvement which merits reassessment is the evaluation and improvement of crown quality.

Crown quality is reflected in the final product through (1) the number, size and distribution of knots and associated defects, and (2) the vigor and productivity of the plant. A number of composite and individual-trait measures of crown quality have been discussed for their potential utility in breeding programs for a variety of species (Campbell 1961, Strickland and Goddard 1965, Bailey et al. 1974, Bannister 1980). The North Carolina State University-Industry Pine Tree Improvement Cooperative employed a six-point subjective scale for the assessment of crown quality in first-generation progeny tests. This crown score incorporated traditional 'crown-form' characteristics as well as individual branch traits into a single measure. Some improvement has been observed in the overall crown quality of progeny from first-generation orchards in loblolly pine (Woessner 1965, J.T. Talbert, pers. comm., 1982), likely a result of the heavy emphasis placed on crown traits in the first round of selection. However, the subjective crown score used in the first generation has been found to have a low repeatability across tree graders and among trials (Paschke 1979), and proved to be very weakly inherited in a 5-year old unselected population of loblolly pine (Stonecypher et al. 1973). Much of the imprecision associated with crown score may result from the subjective nature of the trait. Several branch, crown and foliar characteristics must be evaluated simultaneously by the tree grader in establishing a crown-score value, introducing the potential for differences in interpretation and relative weighting by different graders. This same complexity may also lead to an inflated measurement error for a 'composite' trait in comparison to individually-specified traits. In addition, subjective crown scores have traditionally included traits such as apical dominance, crown shape and foliar density, under the assumption that such traits are important to stem form and knottiness, and plant vigor. Such traits are difficult to define and to measure precisely, and are likely to be accompanied by considerable environmental variation. Since it is of interest to minimize the total number of traits included in a selection program, it may be of value to incorporate only that small number of traits which are the most directly related to plant size, straightness and knot size and density, and which can be measured consistently and accurately.

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The impact of stem knots on product quality and recovery in loblolly pine has been well documented (Von Wedel et al. 1968, Blair et al. 1974, Phillips et al. 1980), but the relationship between crown and branch properties and grade yields across a range of tree sizes and product outcomes has yet to be explored for mature trees. If one or a small number of individual branching traits were to demonstrate at least as strong a relationship with whole-tree value as did crown score, exhibited as good or better heritability, and could be measured accurately and repeatably, then a case could be made for substituting one or more separate branching traits for crown score in loblolly pine selection programs.

MATERIALS AND METHODS

A study was initiated in the autumn of 1982 to evaluate the contribution of various combinations of crown and branch traits to the dollar value of a stem after adjustment for tree height, diameter and stem straightness, and to investigate the repeatability of standing-tree measures of branching properties in comparison with crown score over separate grading trials. The study consisted of two phases. The first phase focused on the development of a model relating the size, form and knottiness of 2.6-meter loblolly pine veneer bolts to the estimated dollar value of those bolts. In the second phase, measurements were taken on standing, and subsequently felled, trees, and these measurements were used to predict whole-tree dollar value based on the relationship derived in Phase I. This whole-tree value could then be regressed on a variety of whole-tree characteristics.

I. Bolt Analysis

Data collected in a 1968 U.S. Forest Service study of veneer recovery from 39 mature North Carolina-source loblolly pines[2/] were used, along with an Autumn, 1982 estimate of relative dollar values of veneer by sheet size and

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[2/] Results from the U.S.F.S. study are discussed by Schroeder and Clark (1970) and by Phillips et al. (1979, 1980). The author gratefully acknowledges their assistance in providing the data.

grade[3/], to construct a regression model relating veneer dollar value for 2.6-meter veneer bolts to bolt dimensions, form and knot traits, to be used in Phase II of the study. Large-end and small-end inside-bark diameters, taper, deflection[4/], total knot number, average knot diameter and the number of knot-free faces had been measured on each of the 226 bolts included in the present study. From this data, Smalian bolt volume and a measure of knots per square foot (KPF)[5/] were calculated for each bolt.

Stepwise regression techniques were used to select the set of bolt traits which predicted bolt dollar value most accurately and precisely. Quadratic terms for both bolt diameters and for deflection were also included in the stepwise analysis. Due to a high degree of intercorrelation among the bolt variables chosen in the stepwise procedure, a principal components analysis was performed on the bolt variables to produce a set of independent and uncorrelated linear combinations of these variables. These components could then be evaluated independently for their influence on bolt dollar value. Components were dropped from the model if they explained little of the variance in the X-space and an insignificant portion of the variability in bolt dollar value. The retained subset of principal components and the partial regression coefficients relating these components to bolt dollar value were then used to calculate biased but more stable estimates of regression coefficients for the original X variables (see Webster et al. 1974).

To test the impact of fluctuations in relative veneer-grade values, and to evaluate the specific effects of an increased premium placed on high-grade veneer, the original relative values applied to full- and half-sheet A/B-grade veneer were multiplied by 1.5, new bolt values were calculated, and biased regression coefficients were recalculated by the methods described above. For simplicity, the two value models will be referred to as V2 and V3, to represent the ratio of A/B to C/D product values in the two models.

II. Whole-Tree Analysis

In the autumn of 1982, 27 mature loblolly pines representing a range of D.B.H., straightness and crown score[6/] values were selected from thinned and unthinned plantations growing at the Schenck Demonstration Forest in Raleigh, North Carolina. All sample trees were chosen to have a similar growing space, and no open-grown trees were included in the study. In addition to D.B.H., straightness score and crown score, the following branching characters were assessed on the standing trees:

1. Branch angle (degrees): 90 is perpendicular to the bole.

[3/] Pricing figures for southern pine veneer were obtained from Random Lengths (October, 1982) and adjusted to the following relative dollar prices: Full-sheet A/B - 1.0; Full-sheet C/D - 0.5; Half-sheet A/B - 0.9; Half-sheet C/D - 0.4; Strip - 0.4; Fishtail - 0.3.

[4/] Measured as the maximum deviation of the bolt surface from a string line stretched across the sweep.

[5/] KPF = KNOT # $\Big/ \left[\left(\frac{\pi}{4}\right) \times \left(\frac{\text{L.E.D.} + \text{S.E.D.}}{2}\right)^2 \times \left(\frac{1}{144}\right) \times \text{BOLT LN.} \times \text{\#CLR. FACES}\right]$.

[6/] Straightness was assessed on a 1 to 5 scale, with 1 being perfectly straight and 5 having severe sweep in two planes. A 1 to 6 crown score was employed with 1 being an 'excellent' crown and 6 representing a 'poor' crown.

2. Branch diameter (1 to 4 scale): 1 is small, 4 is very large, relative to the surrounding stand.
3. Branches per whorl: average number of major branches at a node.
4. Live-branch number: total number of major living branches.
5. Live-crown ratio (percent): crown length/total tree height.
6. Pruning (1 to 3 scale): 1 is good, 3 is poor, relative to the surrounding stand.

Branch diameter and angle and the number of branches per whorl were assessed in the middle-third of the live crown. Crown score and each of the branching traits were assessed a total of three times by two different graders on each sample tree to provide an indication of the repeatability of these traits.

All 27 trees were felled, and measurements taken of total height, length of the living crown, total number of living branches over 1" (2.5 cm.) in diameter, and average branch angle (degrees) and branch diameter (inches) in the middle-third of the live crown. The trees were then delimbed and bucked into 2.6-meter veneer bolts to a minimum 8" (20-cm.) small-end diameter, and the same bolt traits were assessed on each section as had been measured in the U.S.F.S. study. Merchantable height and volume were calculated as the sum by tree of the lengths, or Smalian volumes, of all veneer bolts having inside-bark small-end diameters of at least 8" (20 cm.). These bolt measurements were entered into the stabilized regression equations derived in Phase I, to produce a predicted dollar value by bolt for each of the two veneer-pricing models. Finally, bolt values were summed by tree, yielding a predicted whole-tree dollar value for each of the 27 sample trees under each relative pricing model.

The same stepwise regression techniques and model-selection criteria used in Phase I were employed at the whole-tree level to choose the set of standing-tree traits and the set of felled-tree traits which best predicted tree dollar value under the V2 pricing model for the 27 trees in the study. Crown score, standing-tree branch traits and felled-tree branch traits were examined in separate analyses and compared later. After the best set of predictive variables was chosen, tree dollar values calculated from V2 and V3 were regressed separately on this set of variables. A principal components procedure was again employed to ensure maximum stability of the regression equation; however, none of the components calculated from any of the variable sets met the criteria for exclusion from their respective models. Since principal-components estimates of regression coefficients are identical to ordinary-least-squares estimates for the full-model case, the original least-squares coefficients were retained for all models. Each set of partial regression coefficients was interpreted to be a set of relative economic values for the traits in that model.

Analyses of variance were performed on each of the individual crown and branch traits and on the linear combinations of branch traits which appeared together in the final economic value models. From these analyses, repeatability was calculated as the ratio of tree-to-tree variation in a given trait or combination, over the sum of tree and tree-by-trial variances. Partial correlations were calculated between felled-tree and standing-tree measures of each branch trait, among the standing-tree and among the felled-tree branch traits, adjusted for tree size and straightness, using the GLM/MANOVA procedure of SAS (SAS Institute Inc. 1982). The same techniques were also used to calculate partial correlations between each standing- or felled-tree branch trait and knot number and average knot diameter in the merchantable bole, adjusted for all of the remaining traits in the model.

RESULTS AND DISCUSSION

Bolt dollar value was predicted best in this study by a linear combination of bolt large-end diameter (LED), LED squared, taper, deflection, knot number and average knot width, for both the V2 and V3 veneer-pricing models. Heterogeneity of regression slopes for each variable across trees, across bolt positions, and across 4" (10-cm.) LED classes was tested and found to be nonsignificant at $\alpha = 0.10$. As more emphasis was placed on A/B-grade veneer by shifting from V2 to V3, a significantly greater negative emphasis was placed on knot number and width, reflecting the increasing importance of quality to bolt value.

The principal-components procedure broke the six bolt variables chosen above into six components. One of the components explained a nonsignificant portion of the variation in the X-space and in bolt value for both V2 and V3. The removal of this component increased the coefficient of variation for a given model only slightly (from 23.1% to 24.0% for V2, and from 27.8% to 29.3% for V3), and successfully reduced the standard errors for all six recalculated regression coefficients from their ordinary-least-squares levels. The final equations for V2 and V3 are presented in Table 1.

Table 1. Equations relating bolt dollar value to bolt characteristics under two veneer-pricing models.

VARIABLE	b_{V2}[a]	t[b]	b_{V3}	t
Intercept	-32.28	***	-29.11	***
Large-end diameter	2.82	ns	1.78	ns
$(\text{Large-end diameter})^2$	0.42	***	0.51	***
Taper	-12.47	***	-12.03	***
Deflection	-5.56	*	-6.04	*
Knot number	-0.33	*	-0.51	*
Knot diameter	-3.18	*	-6.53	***

[a] The V2 pricing model assigns twice the relative dollar value to A/B-grade veneer that it does to C/D-grade, while the V3 pricing model applies three times more value to A/B-grade veneer, on a per-thousand-cubic-foot basis.

[b] ns: not statistically different from zero at $\alpha = 0.05$.
*: significantly different from zero at .05 $\leq \alpha <$ 0.01.
***: significantly different from zero at $\alpha \leq 0.01$.

These equations were considered fixed for the remainder of the analysis. When the Schenck-Forest data were entered into the fixed bolt-value equations, predicted dollar values by LED-class corresponded very well with actual dollar values from the same LED-class calculated from the original veneer-recovery study results.

Measurements collected from standing trees on individual branch traits and on combinations of two branch traits tended to be more consistent across trials than did the subjective crown score, as measured by the repeatabilities for these traits. Crown score showed a repeatability of 0.37, as compared to repeatabilities of 0.65, 0.48 and 0.69 for branch angle, branch diameter score and live-branch number. Repeatabilities for the sum of branch angle and branch number (0.62) and for the sum of branch diameter score and branch number (0.63) also exceeded that for crown score.

When predicted whole-tree dollar value was regressed on a variety of whole-tree characteristics, merchantable height alone accounted for 98% of the variability in dollar value for both the V2 and the V3 value models. Total tree height was a much poorer predictor of tree dollar value, both alone and in combination with other traits, than was merchantable height, and so was not included in further analyses. Of all the whole-tree variables measured in the study, the best two-variable predictive model included merchantable height and diameter, and the best three-variable model included straightness score along with these two. This three-variable model will be referred to as the 'base model', because the best models of a given size always were found to include these three variables.

Since the branching and crown traits measured in this study were assumed to impact stem quality, and ultimately stem value, as a result of a correlated impact on merchantable-bole knottiness, two whole-tree knot traits - average knot diameter and KPF - were the first variables to be added to the base model and evaluated for their influence on tree dollar value. KPF did not influence the value of a tree significantly in either the V2 or the V3 models, although its negative impact did increase as more emphasis was placed on high-grade veneer. Average knot diameter contributed significantly to tree dollar value above and beyond the base model. However, this trait had a positive coefficient in both the V2 and the V3 models, suggesting that the impact of knot width on tree value was more a reflection of its strong positive correlation with D.B.H. (r=0.74) and with merchantable height (r=0.69) than of its negative effect on product quality, under the pricing models used here.

The addition of different combinations of standing- and felled-tree branch/crown traits to the base model added little to the ability of the resulting model to predict tree value (Table 2). Felled-tree branch traits, either singly or in groups, yielded poorer predictions of tree dollar value than did the corresponding standing-tree measures or crown score in every case, despite the fact that felled-tree branch traits were better correlated with knot number and knot size in the merchantable bole (Table 3). This may be a result of a particularly strong pattern of intercorrelations among the felled-tree branch traits, and between these branch traits and tree size, which could introduce substantial error into the regression model. Among the standing-tree branch characters, only branch angle proved a significant addition to the base model at α=0.10. No single felled- or standing-tree branch trait was significantly more important to tree dollar value than was crown score. However, a combination of the base model with branch angle and live-branch number was a significantly better predictor of tree dollar value than was the

Table 2. Regression equations relating whole-tree characteristics to tree dollar value predicted from two veneer-pricing models.

VARIABLE	b_{V2}[a/]	t	b_{V3}	t	VARIABLE	b_{V2}	t	b_{V3}	t
Merch. Ht.	13.5	***	13.7	***	Merch. Ht.	14.0	***	14.1	***
D.B.H.	29.8	*	28.4	*	D.B.H.	23.7	*	22.4	*
Strt. Score	-4.1	ns	-2.5	ns	Strt. Score	-6.9	*	-5.4	*
Crown Score	-5.7	ns	-5.7	ns	Branch angle	-0.8	*	-0.5	ns
C.V. ($\hat{Y}_{\bar{X}}$)[b/]	8.9		9.6			5.8		6.4	
Merch. Ht.	13.5	***	13.7	***	Merch. Ht.	13.9	***	14.0	***
D.B.H.	28.0	*	26.0	*	D.B.H.	25.7	*	24.0	*
Strt. Score	-3.6	ns	-2.8	ns	Strt. Score	-7.3	*	-5.9	*
Branch angle	-1.1	*	-0.8	*	Branch diameter	-8.8	ns	-10.3	ns
# Live branches	2.3	ns	1.9	ns	# Live branches	1.2	ns	1.0	ns
C.V. ($\hat{Y}_{\bar{X}}$)	5.6		6.5			6.2		6.6	

a/ The V2 pricing model assigns twice the relative dollar value to A/B grade veneer that it does to C/D-grade, while the V3 pricing model applies three times more value to A/B-grade veneer, on a per-thousand-cubic-foot basis.

b/ C.V. ($\hat{Y}_{\bar{X}}$) is the coefficient of variation of a new prediction of bolt dollar value at the mean of all the X_i.

Table 3. Correlations of standing-tree and felled-tree measures of branch traits with crown score and with size and number of knots in the merchantable bole.

	STANDING-TREE WITH:				FELLED-TREE WITH:	
TRAIT	CROWN SCORE	FELLED	KNOT #	KNOT DIAM.	KNOT #	KNOT DIAM.
Branch angle	-0.42	0.49	-0.08	-0.40	-0.16	-0.18
Branch diam.	0.11	0.24	0.15	0.24	0.15	0.38
Branches per whorl	-0.23	0.32	-0.16	-0.32	-0.58	0.11
# Live branches	0.33	0.44	0.25	-0.10	0.31	-0.14
Branches per foot	0.13	0.28	0.10	0.20	0.11	-0.10
Live-crown ratio	0.19	0.73	-0.12	0.23	0.01	-0.15

base model plus crown score. It was also noted that crown score, when added to the end of each of the best four- and five-variable models (the base model plus one or two branching traits), did little to improve these models. Apparently, once the branch components of crown score are accounted for, little economic benefit is accrued by including crown form components in the value model.

Partial regression coefficients for the best four- and five-variable V2 and V3 models are presented in Table 2. Despite the generally low levels of statistical significance associated with crown and branch traits in all of the models examined in the study, the signs of the regression weights for these traits, and the changes in the impact of these traits on tree value as a greater premium is placed on high-grade veneer, help to explain the role of crown and branch traits in determining tree dollar value. Branch angle in both value models had a negative impact on tree value. This result was initially surprising, since an increasing branch angle (i.e. flatter branches) has been shown to correlate fairly well with decreasing knot diameter. However, branch angle was poorly correlated with knot diameter in the lower two 2.6-meter veneer bolts on a given tree, and these bolts tend to contribute the most to total tree value. Also, branch angle in this study and in previous studies (Faulkner 1969, Strickland and Goddard 1965) has exhibited a consistent negative relationship with tree height, indicating that the tallest trees are often those with the steepest branches. The importance of merchantable height to tree value in this study, combined with the observed negative correlation of merchantable height and branch angle (r=-0.43), could be 'swamping out' any knot-size benefits of increasing branch angle in favor of the height increase correlated to a decreasing branch angle. This conclusion is supported by the positive shift in the impact of branch angle which was observed when a greater value was given to high-grade veneer. The seemingly-contradictory positive relationship of live-branch number with tree dollar value could be explained similarly. Crown score and branch diameter score, both of which associate a higher 'quality' with a decreasing score, are negatively related to tree dollar value, suggesting that these traits might be influencing tree value through an effect on product quality. However, the strong negative correlation of crown score with merchantable height, and the lack of a change in the dollar impact of crown score with a changing emphasis on high-quality products, indicate that this trait likely is affecting tree value only as a function of its correlation with tree size. Only branch diameter score is relatively uncorrelated with tree size, and as a result, is the only trait of the four discussed here that could by impacting tree value primarily by way of stem quality. This trait, however, was not a significant influence on tree dollar value in any of the models examined in the study.

Although the regression weights given to most of the crown and branch traits in this study did not differ significantly from zero, the least-squares coefficient on each variable can be taken to represent the best point-estimate of the dollar-value impact of a unit change in a trait in a multi-trait model. If the variables are standardized by their standard errors, then individual regression coefficients in a given model can be directly compared. In this study, the relative dollar impacts of the standardized traits remained fairly constant regardless of the model in which they appeared. Merchantable height was four to five times more important to dollar value than was D.B.H., which in turn received five to ten times the weight of straightness, five times the weight of crown score, three to five times the weight of branch angle, five to ten times the weight of live-branch number, and five times the weight of branch diameter. However, these standardized relative weightings are directly applicable to a selection index only if the genetic and phenotypic parameters used in the formulation of the index, and the phenotypic measurements ultimately entered into the index formula, are also standardized. In addition, it should be noted that the relative economic values estimated in this study are somewhat specific to the product and pricing criteria used in establishing tree dollar value, although adjustments of 150% in relative veneer grade values in this study did not change the final relative economic values significantly.

CONCLUSIONS

The number and average diameter of knots measured on the surface of loblolly pine peeler bolts significantly impacted the dollar value of veneer coming from those bolts, under a pricing model in which high (A/B) grade veneer was assigned at least twice the value of lower grades. However, when dollar value was predicted for whole trees under the same veneer pricing assumptions, the reduction in product quality associated with increases in knot size and number had an insignificant impact on whole-tree value in comparison with the correlated, positive impact of increasing tree size. For this reason, attempts to increase the quality of peeler bolts indirectly through crown quality improvements either had no effect on tree value or actually related to a decrease in tree value due to correlated decreases in tree diameter and/or merchantable height. This result does not necessarily suggest that crown or branch traits should be rejected out-of-hand as selection criteria in loblolly pine, however. The ultimate weight assigned to any trait in an index selection program depends not only on the relative economic values of the index traits, but also on the heritabilities and the genetic and phenotypic correlations among them. Although estimates of such parameters are not yet available for individual branching traits in mature loblolly pine, heritabilities estimated for these traits in young trees and in other species compare favorably with those estimated for crown score in a young loblolly pine population (Stonecypher et al. 1973). This study has demonstrated for one unselected population of mature loblolly pine that there are combinations of separately-measured branch characters which can be measured easily and more repeatably than a subjective crown score, and which ultimately may relate better to tree dollar value. Relative economic values for size, form and crown or branch traits should be evaluated for other product outcomes and combined with reliable estimates of genetic and phenotypic parameters for these traits in mature trees in a multi-trait index before the final decision is made whether to include crown or branch traits in future rounds of selection.

LITERATURE CITED

BAILEY, J.K., P.P. FERET and D.L. BRAMLETT. 1974. Crown character differences between well-pruned and poorly-pruned virginia pine trees and their progeny. Silv. Genet. 23(6): 181-185.

BANNISTER, M.H. 1980. An early progeny trial in Pinus radiata. 3. Some characters affecting log quality. N.Z.J. For. Sci. 10(2): 325-342.

BLAIR, R.L., B.J. ZOBEL, E.C. FRANKLIN, A.C. DJERF and J.M. MENDEL. 1974. The effect of tree form and rust infection on wood and pulp properties of loblolly pine. TAPPI 57(7): 46-50.

CAMPBELL, R.K. 1961. Phenotypic variation and some estimates of repeatability in branching characteristics of Douglas-fir. Silv. Genet. 10(1): 109-118.

______________ 1963. Phenotypic correlations among branch and upper crown stem attributes in Douglas-fir. For. Sci. 9(4): 444-451.

FAULKNER, R. 1969. Some characters of secondary importance to stem straightness in breeding of conifers. In: Proc. 2nd World Consult. on For. Tree Breeding, IUFRO, Washington

PASCHKE, J.L. 1979. Age-age relationships in loblolly pine. Unpub. M.S. Thesis, Department of Forestry, North Carolina State University

PHILLIPS, D.R., J.G. SCHROEDER and A. CLARK III. 1979. Predicting veneer grade yields for loblolly and slash pine trees. For. Prod. J. 29(12): 41-47.

____ 1980. Reduce pine veneer losses by selecting blocks properly. For. Indust. 107(4): 40-42.

SAS INSTITUTE INC. 1982. SAS User's Guide, Statistics.

SCHROEDER, J.G. and A. CLARK III. 1970. Predicting veneer grade yields for loblolly pine. For. Prod. J. 20(2): 37-39.

SNYDER, E.B. 1961. Measuring branch characters of longleaf pine. SFES Occ. Pap. #184. 4 pp.

STONECYPHER, R.W, B.J. ZOBEL and R. BLAIR. 1973. Inheritance patterns of loblolly pine from an unselected natural population. N.C. Ag. Exp. Sta. Tech. Bull. #220. 60 pp.

STRICKLAND, R.K. and R.E. GODDARD. 1965. Inheritance of branching and crown characteristics in slash pine. In: Proc. VIII SFTIC: 57-63.

VON WEDEL, K.W., B.J. ZOBEL and C.J.A. SHELBOURNE. 1968. Prevalence and effects of knots in young loblolly pine. For. Prod. J. 18(9): 97-103.

WEBSTER, J.T., R.F. GUNST and R.L. MASON. 1974. Latent-root regression analysis. Technometrics 16: 513-522.

WOESSNER, R.A. 1965. Growth, form and disease resistance in four-year-old control- and five-year-old open-pollinated progeny of loblolly pine selected for use in seed orchards. Tech. Rep. #28, Dept. of Forestry, North Carolina State University.

CONCEPTS FOR ANALYSIS OF INTERGENOTYPIC COMPETITION IN FOREST TREES

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Abstract.--Area Potentially Available (APA), an index of individual-tree competitive status or available growing space, is adapted for use in the analysis of growth response to inter-genotypic competition in genetic field tests. The approach allows geneticists to detect differential response to competition from neighboring trees that vary in size and distance as well as genetic identity. Methods for detecting interactions between genetic entities in response to competition are presented. Data from a loblolly pine progeny test planted in a Nelder's Wheel design are used to illustrate the approach.

INTRODUCTION

Competition between trees is universally assumed to operate in closed stands of forest trees. Clements et al. (1929), in a review of the early history of competition, noted that foresters were among the first to recognize competitive effects and to attempt to control competition for commercial benefits through thinning practices. Foresters today regulate inter-tree competition within forest stands to attain full utilization of forest sites and to shape the diameter distribution and form of crop trees.

Competition between crop plants is also of vital concern to agronomists, for they have discovered that the highest yields per acre are generally attained when the competition between plants is high (Donald, 1961). Crop breeders recognize that modern crop varieties must have the ability to grow under extreme density stress, and they have adjusted their selection, breeding, testing, and deployment techniques accordingly.

In tree improvement programs, much less attention has been given to competition -- either as a source of improving per acre yields or as a possible source of error in selection, breeding, and testing. Generally, forest geneticists select outstanding individual trees and test their progeny in field tests wherein many progeny are mixed together, with each progeny replicated either in single-tree plots, row plots of 2-8 trees, or in small rectangular or square plots of 4 to 64 trees. The spacing between trees is generally held constant and wide.

In such tests, the various progenies generally exhibit different growth rates very early -- long before competition between trees can fully develop -- and therefore these growth rate differences do not represent differential response to competition from neighboring trees. Nevertheless, the faster growing progenies do gain a competitive advantage over their slower growing neighbors because they capture a larger share of the site before competition develops. However, progenies selected for vigorous pre-competition growth may not grow well after competition fully develops and neighboring trees begin to compete for limited light, water, and nutrients.

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If progenies differ in their response to competition from neighboring trees, then early evaluation of progeny performance could lead to errors in selection, breeding, and deployment of genetic material in operational plantings where competition is unavoidable as well as desirable for most of the commercial rotation. Moreover, if differences between progenies in their response to competition do exist, it is conceivable that geneticists could exploit such differences for commercial advantage.

Considerations such as these raise fundamental questions that can only be answered through experimentation. One approach, often used in crops, is to carefully design competition experiments wherein large plots of single and mixed progenies are established and grown through rotation age. The yields on a per acre basis are then analysed using an adaptation of the analysis for a diallel mating design (Willey and Heath 1969, Mead 1979). This and similar approaches have occasionally been used in forest trees, but only for seedling experiments (Adams _et al_. 1973, Adams 1980, Cannell 1982, Tauer 1975, Snyder and Allen 1971, and Wearstler 1980).

A less common approach is based on individual-plant competition experiments wherein the number, spatial pattern, and genotype of competing plants is systematically varied to create competitive situations of various types. Growth data are then analyzed using some form of a competition index designed to quantify the competitive situation under which the individual plant responded (Mead 1968, 1979, Willey and Heath 1969).

Most progeny tests, although not designed as individual-tree competition experiments, exhibit many of the features of such experiments. The complex mixtures of genetic entities combined with their differential growth and survival rates before competition create a variety of competitive situations. Once competition begins and growth data are collected in these tests, it should be possible to extract information regarding the response of individual trees to competition from neighboring trees, and to identify those situations in which the genetics of the subject tree or its competitors is a factor in that response.

Concepts and methods are developed in this paper that may allow geneticists to extract such information from genetic field tests. The application of the proposed methods is illustrated with data from a complex genetic field test in loblolly pine (_Pinus taeda_ L.).

METHODS

The fundamental problem in assessing individual-tree response to competition is the development of an index of local density in the neighborhood of an individual tree. Such an index should properly account for the size of the subject tree and the size and spatial pattern of neighboring trees; and it should both reflect the current competitive status of the subject tree and changes in that status over time. Fortunately, such an index exists in the form of the APA (Area Potentially Available) index first introduced by Brown (1965) and later modified by Moore *et al.* (1973) and also by Mead (1965).

The APA index.--The APA index is defined as the area of an irregular polygon constructed around a subject tree. The polygon is formed by intersecting lines (influence lines) that are located between and perpendicular to the lines connecting the subject tree and each of its competitors. The area of the polygon around a subject tree represents the "relative growing space" or "competition status index" of the subject tree within the stand as limited by its neighbors. This area is mutually exclusive to that of any other tree, and the sum of the areas for all polygons represents the total area utilized by the stand.

The APA index has recently been compared with several other competition indices by Daniels (1981), who concluded that the APA index was superior to all those tested for predicting future basal area growth in a long-term loblolly pine spacing trial. A FORTRAN computer program written by Daniels (1981), called COMP5, was enhanced by the present authors for use in genetic field trials with any arbitrary spatial design and genetic structure. Basically, the enhancements to COMP5 included: (1) additional code to keep up with the genetic identity of all trees, and (2) the addition of a new index of relative influence (RI), useful in detecting genetic interactions.

Computation of the APA index: program COMPAPA.--The program initiates a search for influential competitors around each subject tree; assembles a prospective list of those trees which could influence the construction of the subject tree's polygon; computes all possible intersections of each competitor's influence lines with one another; and then constructs the polygon using a minimum subset of competitors. Further details regarding the methods used appear in Daniels (1981), and in the program itself which is available on request.

In this study relative basal area was used as the weighting factor to locate the influence lines between the subject tree and each competitor (Moore *et al.* 1973), which is computed as:

$$LP = \frac{D_S^2}{D_S^2 + D_C^2} \times L$$

where LP = the distance from the subject tree to the competitor's line of influence,

L = the distance from the subject tree to competitor,

D_S = d.b.h. of subject tree (in inches), and

D_C = d.b.h. of competitor (in inches).

Note that when subject and competitor are of equal d.b.h, $LP = 1/2\ L$; and that LP is inversely related to the influence of competitor on subject tree.

The FORTRAN code necessary to maintain the genetic identity of the subject tree and each of its competitors is quite simple, but, in order to use this information to detect genetic interactions, a measure of influence must be constructed to quantify the relative competitive pressure exerted by competitors of a given genetic identity on a subject tree.

An index of relative influence.--An index of relative influence should provide additional information about the relative influence of a competitor with respect to the other competitors used in constructing a subject tree's polygon. This index should be independent of the area of the polygon itself, because it is desirable to compare relative influence values for different genetic entities across a wide range of local densities. Of the several alternatives considered, the following index appears to satisfy the above objectives:

$$RI_{A/B} = \frac{\sum_{B} (1/LP_j)}{\sum_{i=1}^{j} (1/LP_j)} \qquad (0 <= RI_{A/B} <= 1)$$

where LP is previously defined, and

$RI_{A/B}$ = relative influence of all competitors from genetic entity B surrounding the subject tree with genetic identity equal to A,

$\sum_{i=1}^{j} (1/LP_j)$ = the sum of the inverse LP distances for all competitors influencing the subject tree, and

$\sum_{B} (1/LP_j)$ = the sum of the inverse distances for all competitors genetic type B influencing the subject tree.

Note that the proposed relative index has the following properties:

1. in a genetic test with a mixture of n genetic entities, there are n relative index values for each subject tree,

2. the sum of all RI values for a given subject tree is always equal to unity,

3. an RI value of zero indicates that no competitors of the given genetic type influenced the subject tree,

4. an RI value of unity indicates that all competitors influencing the subject tree were of the given genetic type, but not necessarily of the same genetic type as the subject tree, and

5. an RI value of unity with the form $R_{A/A}$ indicates a situation in which the subject tree and all of its competitors are of the same genetic type.

It is convenient to refer to polygons of the type referred to in (5) as "pure polygons," as opposed to all others which are "mixed polygons." Figure 1 illustrates the construction of the APA polygon and the associated relative index.

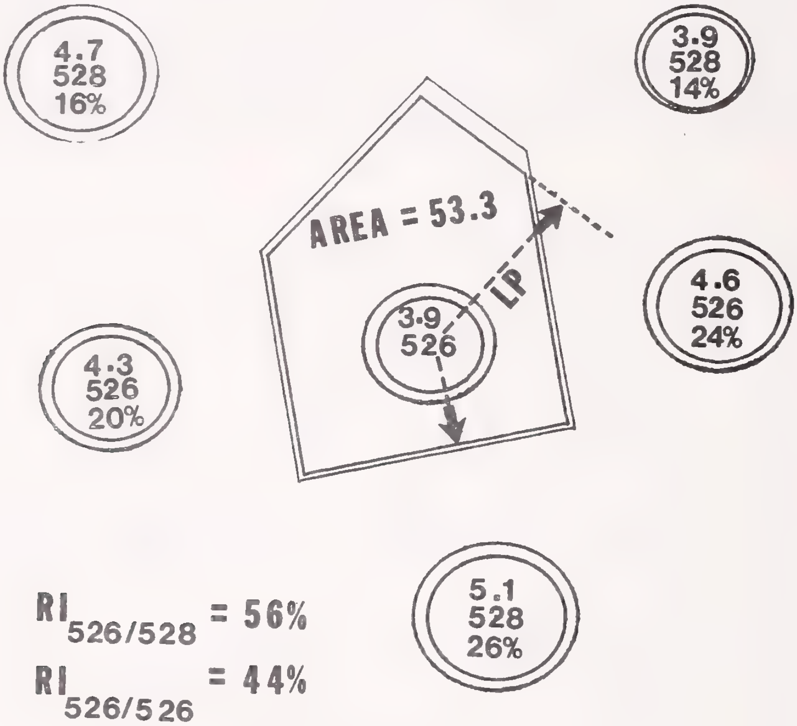

Figure 1.--APA and Relative Influence indices for a typical situation. The inner circles represent diameters at breast height at age 7. In each circle, the top number is the d.b.h. in inches, the middle number is a family I.D., and the lower number is the percent relative influence of the competitor on the subject tree at age 7. The outer circles represent the d.b.h. of each competitor the following year (8). The inner polygon corresponds to year 7, and the outer to year 8.

Regression models to assess response to competition.--Given that APA and RI indices have been computed for each tree in a genetic test, it is then possible to attempt an analysis of the data with the objective of exposing any differences between genetic entities in response to competition. Multiple linear regression models appear to be satisfactory for this objective, at least as a preliminary to more sophisticated (and perhaps more appropriate) methods such as multivariate analyses.

Consider a stand of trees in which individual-tree attributes such as diameters, heights, and crown ratios have been measured for each tree at some initial time (t0). A simple regression model for the prediction of basal area growth of individual trees between time t_0 and some future time t1 might appear as follows:

(1) $BAG_{t0-t1} = \mu + \beta_1(BAS_{t0}) + \beta_2(HTS_{t0}) + \beta_3(CRS_{t0})$

where

μ = the mean basal area growth for all trees

BAS_{t0} = the basal area of the subject tree at time t0

HTS_{t0} = the total height of the subject tree at time t0

CRS_{t0} = the ratio of live crown to total height for the subject tree at time t0

and μ, β_1, β_2, and β_3 are least squares coefficients.

This model takes account of the current size and crown development of an individual tree in predicting future growth. Models like this are common in forest growth and yield formulations and perform well in forest stands if the prediction interval (t1-t0) is less than about 5 years. Generally, larger trees with higher crown ratios produce more basal area increment than their smaller counterparts with less crown.

Model 1, even though it might have practical utility, ignores the local density regime experienced by the subject tree. Consideration of APA for the subject tree is added as follows:

(2) $BAG_{t0-t1} = \mu + \beta_1(BAS_{t0}) + \beta_2(HTS_{t0}) + \beta_3(CRS_{t0}) + \beta_4(APA_{t0})$

= model 1 + APA component

where

APA_{t0} = Area Potentially Available at time t0 for the subject tree (as defined in the previous section), β_4 is a coefficient to be estimated, and

all other terms are previously defined.

The predictive power of the model can now be expected to increase if, indeed, inter-tree competition is a factor in tree growth. Daniels (1981) found this to be the case in his work, noting that APA was the only index powerful enough to add significantly to the prediction of basal area growth in the presence of the other predictors. The coefficient β_4 will generally be positive, and represents the average capacity of individual trees to respond to growing space limits imposed by neighbors.

Note that the residuals from prediction in both models 1 and 2 may be related to the tree's genotype as well as interactions with competing trees of other genotypes in the case of mixed plantations.

At this point, allowance is made for mixtures of several genetic entities in a test plantation. The equivalent of model 1 allowing for genetic differences (with t0 and t1 subscripting now dropped for brevity) is:

$$(1A)\quad BAG = \mu + \sum_i \alpha_i \lambda_i + \beta_1(BAS) + \beta_2(HTS) + \beta_3(CRS) + \beta_{1i}(BAS_i) + \beta_{2i}(HTS_i) + \beta_{3i}(CRS_i)$$

where BAG, BAS, HTS, and CRS were previously defined, and

$\Sigma\alpha_i\lambda_i$ = a set of indicator variables (λ_i) and their least squares coefficients (α_i),

λ_i = 1 when the subject tree's genetic identity is i and 0 otherwise,

$BAS_i = \lambda_i(BAS)$, $HTS_i = \lambda_i(HTS)$, and $CRS_i = \lambda_i(BAS)$.

As before, β_1, β_2, and β_3 designate the least squares coefficient for the general effect of either BAS, HTS, or CRS on basal area growth for the whole population, and their subscripted counterparts designate specific differences in the response of genetic entity i with respect to the general response. This model is a specialized form of a covariance model in which BAS, HTS, and CRS are the covariates, λ_i are the qualitative design variables (in this case genetic entity), β_1, β_2, and β_3 represent the general regression slope for all trees regardless of genetic origin, and the subscripted coefficients β_{1i}, β_{2i}, and β_{3i} represent specific slopes for each genetic entity. However, unlike many applications of covariance analyses, the goal is not to "adjust" means, but rather to expose genetic differences in terms of the β coefficients associated with variables such as BAS_i, HTS_i, and CRS_i.

Similarly, model 2 can be made sensitive to genetic differences,

$$(2A)\quad BAG = \mu + \sum_i \alpha_i \lambda_i + \beta_1(BAS) + \beta_2(HTS) + \beta_3(CRS) + \beta_4(APA) + \beta_{1i}(BAS_i) + \beta_{2i}(HTS_i) + \beta_{3i}(CRS_i) + \beta_{4i}(APA_i)$$

with the same interpretation, except that APA has been added as an additional predictor. In this model, it is recognized that there is a general relationship between basal area growth (BAG), current tree size (BAS and HTS), crown development (CRS), and competitive status (APA). The goal is to detect any genetic difference in these relationships that would allow a better prediction of future growth knowing the genetic identity of the subject tree; and this sensitivity is provided by the addition of the subscripted terms.

To this point, the genetic identity of surrounding trees has been ignored, which could be a source of error in the models so far presented. The $RI_{A/B}$ index developed earlier is used to include a general relative influence effect of a genetic entity as a competitor as follows:

$$(3)\quad BAG = \mu + \sum_i \alpha_i \lambda_i + \beta_1(BAS) + \beta_2(HTS) + \beta_3(CRS) + \beta_4(APA) + \beta_{1i}(BAS_i) + \beta_{2i}(HTS_i) + \beta_{3i}(CRS_i) + \beta_{4i}(APA_i) + \sum_j \beta_{5j}(RI._{/j})$$

where

$RI._{/j}$ = the general relative influence of genetic entity j as competitor (ignoring the genetic identity of the subject tree),

and β_{5j} are least squares coefficients.

The β_{5j}'s are not subscripted by i, reflecting the fact that in this model the genetic identity of the subject tree is ignored, as the goal is to fit a general relative influence effect for each genetic entity as competitor, disregarding the genetic identity of the subject tree. The interpretation of this model is similar to the preceding model 2A, except that now allowance is made for the possibility that genetic entities may not influence the growth of subject trees in the same way. Negative values of β_{5j} indicate a negative influence on the growth of subject trees, positive values a positive influence, and zero (or nonsignificant values) no influence.

As a final genetic refinement to the model, allowance is made for the possibility that specific genetic interactions of subject and competitor could account for some of the variation in the basal area growth of individual trees by the following model:

$$(4) \quad BAG = \mu + \sum_i \alpha_i \lambda_i + \beta_1(BAS) + \beta_2(HTS) + \beta_3(CRS) + \beta_4(APA) + \beta_{1i}(BAS_i) + \beta_{2i}(HTS_i) + \beta_{3i}(CRS_i) + \beta_{4i}(APA_i) + \sum_i \sum_j \beta_{6ij}(RI_{i/j})$$

where the general influence terms (β_{5j}'s) are replaced by specific influence terms (β_{6ij}'s) which account for the genetic identity of both subject and competitor. This form represents an explosion of coefficients, and unless the field test is quite large it may not be possible to fit the model. For example, with only 8 genetic entities, the number of coefficients (prior to restrictions placed to eliminate dependencies) for models 1, 2, 1A, 2A, 3 and 4 are 4, 5, 36, 45, 53, and 109 respectively.

Model 4 appears to be detailed enough to expose genetic differences in density response in even the most complex genetic field tests. To illustrate the application of these methods, they are applied in the next section to a loblolly pine progeny test with a complex structure.

MATERIALS

Seventh- and eighth-year measurements of d.b.h., total height, and crown length for loblolly pines planted in a Nelder's design[2] (Nelder 1962) were used to illustrate the application of the methods developed in the preceding sections. The planting site is in northeast Mississippi (Oktibbeha County, 33' 18" North latitude, 88'47" West longitude). Open-pollinated families from eight clones in the Weyerhaeuser Company seed orchard at Aliceville, Alabama, are represented in the test. Four of these clones (8-507, 8-509, 8-530, and 8-532) are from ortets in Lamar County, Alabama, two clones (8-505 and 8-519) are from Pickens County, Alabama, and two clones (8-526 and 8-528) are from Greene County, Alabama.

This study used six replicates, with each replication represented by one circular Nelder's Wheel. A wheel consists of 40 measurement spokes, 2 border spokes, and 7 planting positions along a spoke. The inside and outside positions are borders, so there are five measurement positions having the following spacings and trees per acre: 6 feet x 6 feet (1210 trees/acre), 6.8 feet x 6.8 feet (938 trees/acre), 7.7 feet x 7.7 feet (727 trees/acre), 8.8 feet x 8.8 feet (563 trees/acre), and 10 feet x 10 feet (436 trees/acre). Only a single family is planted along a spoke. Families are assigned to adjacent spokes in a particular order to provide competition among trees of only a single family on all sides, competition with trees of the same family on three sides and with a tree of a different family on the fourth side, and competition with trees of a different family on two sides.

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[2] From a cooperative study between Mississippi State University and Weyerhaeuser Company. The contribution of personnel and genetic material by Weyerhaeuser Company for establishment of the planting is acknowledged.

RESULTS AND DISCUSSION

APA was computed for each non-border tree in the study based on the 7th-year data (Figure 2). Trees exposed by the death of a border tree were treated as border trees in the analysis. The number of competitors influencing each subject tree ranged from 4 to 10, with 5 or 6 being typical. The total number of non-border trees was 1,010; and the number of trees per spoke x family combination ranged from 21 to 30. The means (on a per-tree basis) across all replicates for BAS, HTS, CRS, APA and BAG for each family and position for age 7 appear in Tables 1 and 2 respectively.

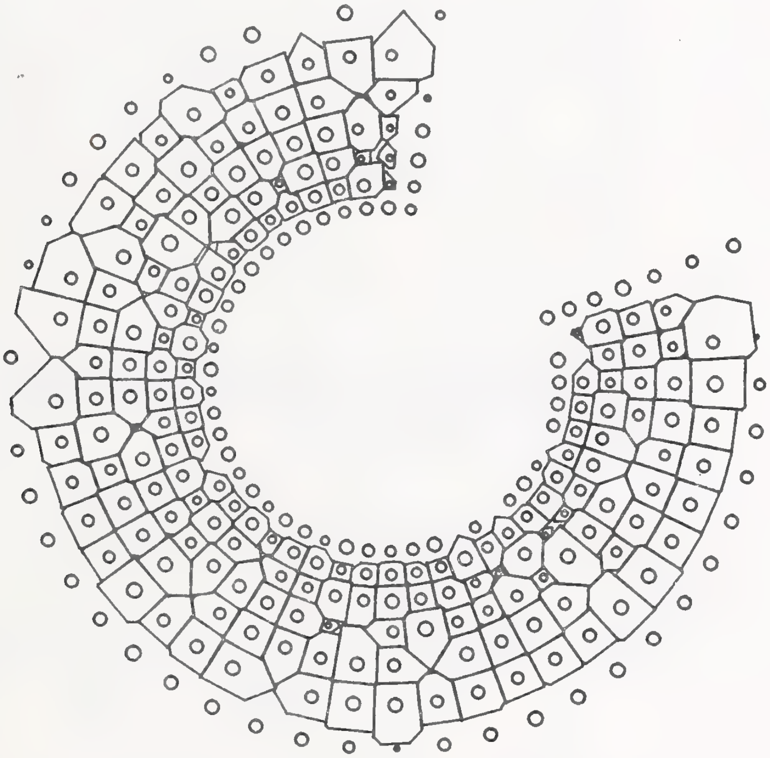

Figure 2.--APA polygons constructed around each non-border tree in one replicate of a Nelders Wheel. The diameters of the circles are proportional to the d.b.h. of living trees.

Table 1.--Means on an individual-tree basis over 6 replications of the Nelder's Wheels by family at age 7 years

	FAMILY							
Variable	505	507	509	519	526	528	530	532
BAS (ft^2)	0.065	0.069	0.053	0.062	0.063	0.066	0.067	0.065
HTS (ft)	18.64	19.29	17.03	18.04	18.92	19.21	19.12	18.84
CRS	0.792	0.801	0.797	0.783	0.808	0.792	0.795	0.798
APA (ft^2)	63.23	70.85	66.23	72.39	70.56	69.87	73.31	73.71
BAG (ft^2)	0.036	0.038	0.036	0.034	0.040	0.036	0.041	0.039

Table 2.--Means on an individual-tree basis over 6 replications of the Nelder's Wheels by density at age 7 years

	PLANTING DENSITY				
Variable	1210	938	727	563	436
BAS (ft^2)	0.055	0.060	0.064	0.068	0.071
HTS (ft)	18.86	18.73	18.56	18.60	18.50
CRS	0.761	0.780	0.796	0.820	0.825
APA (ft^2)	35.03	52.20	66.42	87.63	110.56
BAG (ft^2)	0.026	0.030	0.038	0.043	0.051

Relative influence indices were computed according to the procedures given previously. Since there were 8 families, there were 8 RI values per tree, although typically only 1 (a "pure polygon") or two (a "binary polygon") influence values were non-zero. Occasionally 3, but never 4 influence values were non-zero.

Table 3 summarizes the various models as fit to this data set. Any two models in this table can be compared by considering the model with the most terms the "full" model, and the one with the fewer terms the "reduced" model. The following F-test (Neter and Wasserman, 1974) is appropriate for testing the null hypotheis that the coefficients of all the additional terms in the full model are equal to zero:

$$F = \frac{(SSE(R) - SSE(F))/(edf(R)-edf(F))}{SSE(F)/edf(F)}$$

where

SSE(R) = residual sum of squares for the reduced model
SSE(F) = residual sum of squares for the full model
edf(R) = residual degrees of freedom for the reduced model
edf(F) = residual degrees of freedom for the full model

This test (at the 0.05 probability level) applied to table 3 results in the following, based on the prediction of 7-th year basal area growth:

1. APA by itself is a significant predictor of BAG,
2. BAS, HTS, and CRS are significant predictors of BAG,
3. APA adds significantly to BAS, HTS, and CRS,
4. APA$_i$ adds significantly to BAS, HTS, CRS, and APA, and
5. neither BAS$_i$, HTS$_i$, CRSi, $R_{.}/j$, nor R_i/j add significantly to (4).

Table 3.--Summary of regression models for prediction of 7-th year basal area growth

Components Included													Residuals	
Mean	λ_i	BAS	HTS	CRS	APA	BAS$_i$	HTS$_i$	CRS$_i$	APA$_i$	$R_{.}/j$	R_i/j	R^2	SS	d.f.
*					*							0.46	0.159	1008
*		*	*	*								0.35	0.194	1006
*	*	*	*	*	*							0.51	0.145	998
*	*	*	*	*	*				*			0.52	0.142	991
*	*	*	*	*	*	*	*	*	*			0.53	0.140	970
*	*	*	*	*	*				*	*		0.52	0.141	984
*	*	*	*	*	*	*	*	*	*	*		0.53	0.138	963
*	*	*	*	*	*				*		*	0.54	0.136	942

Hence, the only genetic component that contributed significantly to the prediction of basal area growth in this data was APA_i, indicating that families differed in their use of growing space for basal area growth. Only two APAi coefficients were significant -- those for families 526 and 519. Family 526 had a significant positive coefficient whereas family 519 had a significant negative coefficient. This indicates that trees from family 526 were relatively efficient users of growing space while trees from family 519 were relatively less efficient than trees from the whole population.

An inspection of Table 1 tends to confirm these results. Family 526, which ranked 6th from the top in terms of average basal area per tree across all densities, and also 6th in APA, ranked 2nd in basal area growth per tree. Family 519, which ranked 7th in basal area, but a surprising 3rd in APA, ranked 8th in basal area growth. Interestingly, family 526 also ranked first in crown ratio.

To further investigate the family differences in the relationship of APA to basal area growth, separate simple linear regressions of BAG over APA were fit using data of subject trees from the same family. The results are given in Table 4.

The regression for family 526 not only had the steepest slope relating basal area growth per square foot of APA, but it also had the highest R^2. Also, the regression for family 519 had the smallest slope, but the R^2 was relatively low. Because the polygons in each of the above regressions included pure as well as mixed types, the pure cases were separated and fitted also. The results are presented in Table 5.

Table 4.--Simple linear regression coefficients of BAG over APA for mixed and pure polygons combined

Family	No. Obs.	Slope	R^2
505	137	0.27689	0.4377
507	125	0.28528	0.4895
509	124	0.24053	0.3026
519	113	0.23582	0.3121
526	132	0.34866	0.5814
528	127	0.29148	0.4601
530	124	0.27900	0.3840
532	128	0.32896	0.5315

Table 5.--Simple linear regression coefficients of BAG over APA for pure polygons alone

Family	No. Obs.	Slope	R^2
505	24	0.19870	0.4682
507	23	0.35825	0.5641
509	14	0.38807	0.0815
519	17	0.28478	0.5769
526	23	0.39643	0.7235
528	22	0.36406	0.5182
530	18	0.27269	0.3388
532	28	0.35440	0.5854

Here the slopes are generally somewhat steeper and the R^2 values higher. However, the correspondence between the two types is quite close, even though the number of trees involved in the latter regressions is small. These results tend to confirm the lack of interactions between families noted previously.

Although the differences exposed in this analysis are not large, they do illustrate that the methods may have utility in exposing this kind of information in other progeny tests. It should be emphasized that the methods proposed and applied here, even though they appear to be useful, are nonetheless preliminary and require further development. It is especially important to apply the methods to other data sets in which different sets of families are tested under a variety of designs.

Further research in this area may provide at least partial answers to the following questions:

1. Do progenies differ in their ability to respond to competition created by neighboring trees?

2. Is that response conditioned by the genetic makeup of the competitors in addition to size and spatial pattern?

3. What is the heritability of this trait?

4. What is the genetic correlation between this trait and pre-competitive growth rate?

5. How do these traits relate to per acre yield capacity?

6. What is the ideal combination of these two traits for commercial forest production?

7. How do progenies that differ in these traits perform when planted alone? In mixtures with other progenies which differ (and perhaps interact) in one or both of these traits?

8. In short, what changes (if any) should be made in selection, breeding, testing, and deployment of genetic material in light of competition effects?

LITERATURE CITED

Adams, W. T. 1980. Intergenotypic competition in forest trees. In: Proceedings of the Sixth North American Forest Biology Workshop (B. P. Dancik, K. O. Higgenbotham, eds.). The Univ. Alberta.

Brown, G. S. 1965. Point density in stems per acre. Forest Res. Inst., N.Z. Forest Service, Forest Res. Notes No. 38, 11p.

Cannell, M. G. R. 1982. 'Crop' and 'isolation' ideotypes: evidence for progeny differences in nursery-grown Picea sitchensis. Silvae Genet. 31: 60-66.

Clements, F. E., J. E. Weaver and H. C. Hanson. 1929. Plant competition -- an analysis of community function. Publ. No. 398. Carnegie Institute, Wash., D.C. 340 pp.

Daniels, Richard F. 1981. An integrated system of stand models for loblolly pine. Ph.D. dissertation, VPI & SU, Blacksburg, Virginia (University Microfilms, Ann Arbor, Michigan). 105 p.

Donald, C. M. 1961. Competition among crop and pasture plants. Adv. Agron. 15: 1-118.

Mead, R. 1965. A relationship between plant-spacing and yield. Annals of Botany 30: 301-309.

Mead, R. 1979. Competition experiments. Biometrics 35: 41-54.

Moore, J. A., C. A. Budelsky, and R. C. Schlesinger. 1973. A new index representing individual tree competitive status. Can. J. For. Res. 3:495-500.

Nelder, J. A. 1962. New kinds of systematic designs for spacing experiments. Biometrics 18: 283-307.

Neter, John and William Wasserman. 1974. Applied Linear Statistical Models. R. D. Irwin, Homewood, Illinois. 842 p.

Snyder, E. B. and R. M. Allen. 1971. Competitive ability of slash pine analysed by genotype x environment stability methods. In: Proceedings 11th Southern Forest Tree Improvement Conference, p. 142-147.

Tauer, C. G. 1975. Competition between selected black cottonwood genotypes. Silvae Genet. 24: 44-49.

Wearstler, K. A. 1980. Competition-density effects and genetic improvement of yield components in loblolly pine (*Pinus taeda* L.) Ph.D. dissertation, North Carolina State University, Raleigh, North Carolina.

Willey, R. W. and S. B. Heath. 1969. The quantitative relationships between plant population and crop yield. Advances in Agronomy 21: 281-321.

A MULTIPLE-OBJECTIVE FOREST TREE BREEDING STRATEGY

Samuel B. Land, Jr. and T. H. Mattheiss[1]

Abstract.--A unique concept is proposed for application of multiple-objective linear programming techniques to tree breeding programs. The concept would retain genetic diversity in the breeding population, permit changes in breeding objectives without returning to earlier generations of selection, and still provide for genetic improvement in any selected direction. Problems with inbreeding are considered, and application of the concept to current tree improvement programs is discussed.

Additional keywords: Multiple-objective linear programming, selection method, selective breeding, tree improvement.

Plant breeders working to increase food and fiber productivity are constantly faced with the problem of how to selectively breed for improvement of many traits simultaneously and yet retain the flexibility to change breeding objectives (directions of improvement). Flexibility in objectives comes from maintaining or incorporating genetic diversity in the breeding population, but this diverts resources away from the short-term maximization of genetic improvement for a single objective.

Present multiple-trait improvement procedures in plant and animal breeding include tandem selection, independent culling levels, and selection indices (Hazel and Lush 1942). All of these procedures are directed toward a single breeding objective. When objectives are initially poorly defined or change in future generations, the breeder often must go back to ancestor populations (if they still exist) to obtain the needed germplasm. This is both inefficient over the long run and impractical for plants that have long generation intervals. Furthermore, the gradual loss of genetic diversity from selection for the same objective over many generations can have disastrous consequences in crop vulnerability.

More conservative, but less efficient, breeding strategies have been followed for forest trees than for annual crops (Namkoong 1970). Recently, multiple breeding populations, or sublining, have been proposed to increase the efficiency of selection indices for trees (Namkoong 1976) and to solve inbreeding problems (Talbert 1979). However, these procedures still are directed toward trait improvement for a single objective.

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Recent advances in mathematical programming techniques suggest that multiple-objective linear programming (MOLP) can be effectively used in directing multi-trait, multiple-objective genetic improvement programs. Kung et al. (1975) noted this potential for forestry seed orchards. The approach represents a new option for breeders, and much work must be done on genetic theory and computer programs before it can be implemented.

This paper describes how the MOLP techniques might be used in forest genetic improvement programs. These new techniques can help tree breeders establish and maintain genetically diverse, flexible breeding populations in an efficient manner while continuing to accomplish genetic improvements for specific objectives.

THE PROPOSED CONCEPT

Schematic Representation of the Breeding Strategy

The breeding population is kept separate from the production (seed orchard) population, as shown in Figure 1 and discussed by Franklin (1975). Up to 15 traits may be considered simultaneously for recurrent selective breeding. These traits can include different variables, such as growth and disease resistance, and different extremes of the same variable, such as high and low wood specific gravity. Potential breeding trees are measured for each trait, either phenotypically or genotypically, and indexed in the multiple-trait space (Figure 2a). The convex hull of the candidates is found and MOLP applied to find the efficient frontier of all trees in that trait space (Figure 2b). Adjacent candidate trees on the frontier (trees 2 and 4, 4 and 9, and 9 and 10 in Figure 2a) are designated for controlled crosses with each other. Note that crosses are not made among breeding trees whose trait combinations fall interior to the convex hull. Furthermore, any "enrichment" of the breeding population by introduction of new genetic material during advanced generations (Franklin 1975) will require that the new material first be progeny tested in a new breeding population, or subline. Candidates on the frontier of this subline population will then be crossed with corresponding candidates of the original breeding population.

The offspring from the controlled crosses will provide the potential breeding trees for the next generation. These trees will again be mapped in the multitrait space, and another MOLP will be solved to identify candidate trees and crosses for the next successive generation (Figure 2c). The candidate crosses may be screened by filter programs to reduce crosses among related individuals and thereby minimize inbreeding buildup. Additional filter programs can be utilized to avoid expanding numbers of candidates and crosses over successive generations.

No economic or heritability weights will be used in the MOLP breeding strategy, since the procedure involves only the breeding population and aims at maximizing gains for all breeding objectives

MODEL OF RECURRENT SELECTION PROGRAM

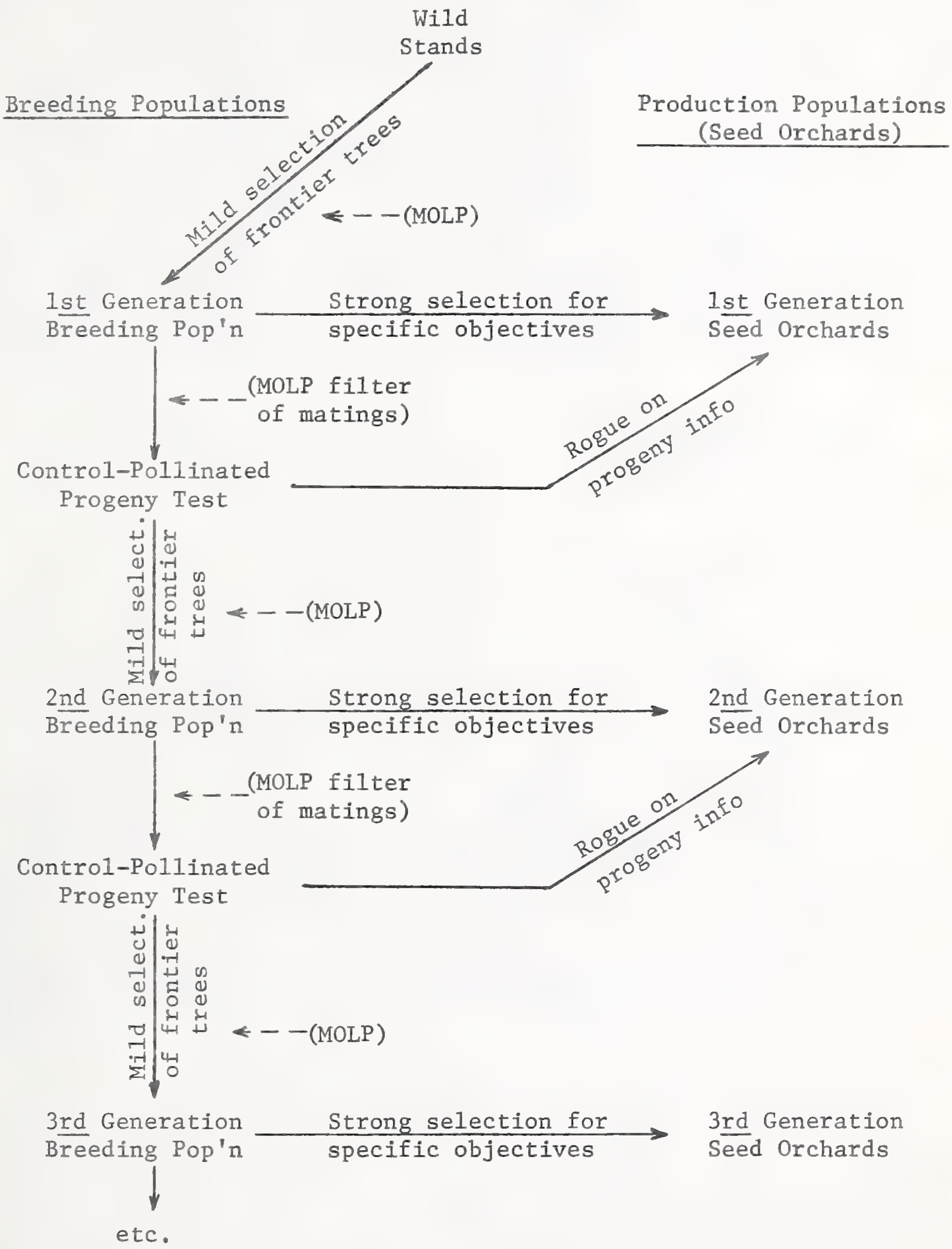
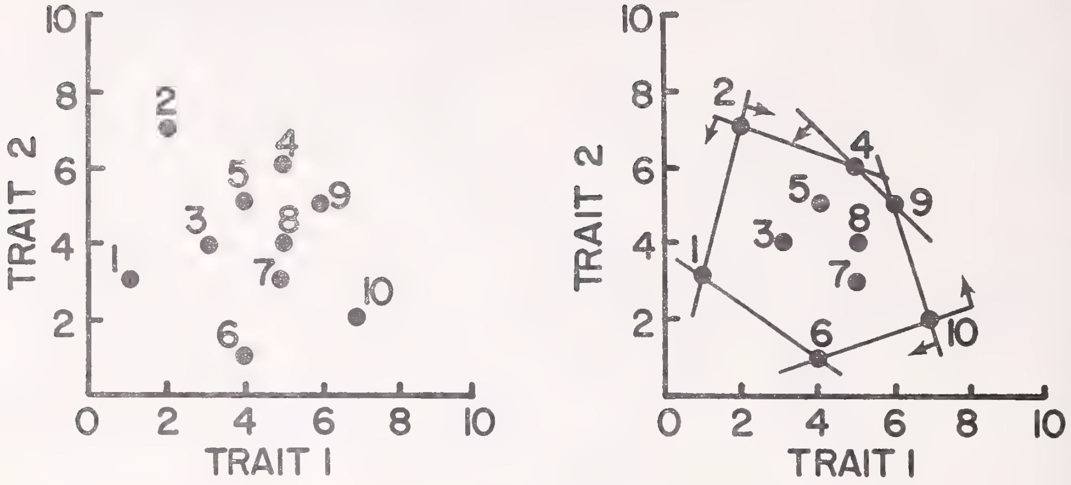
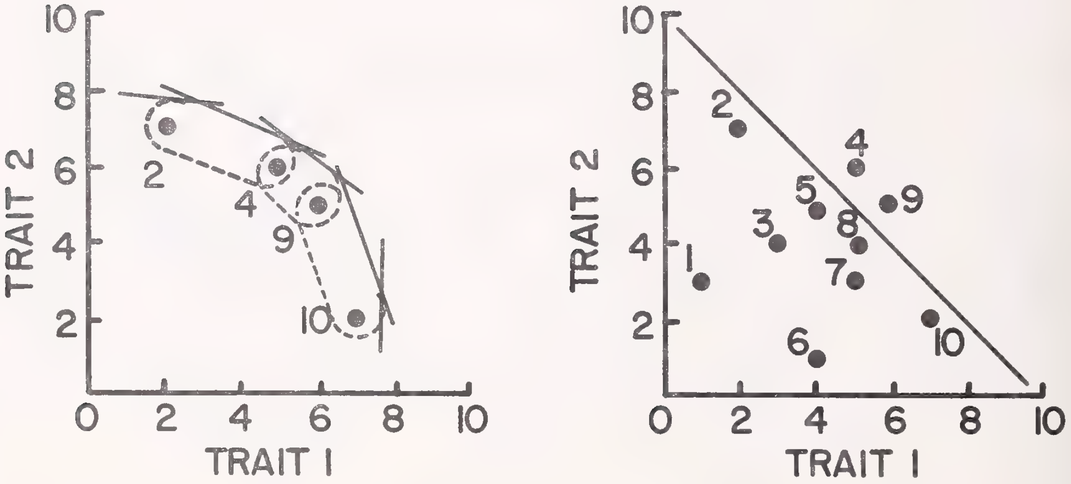

Wild Stands
Breeding Populations
Production Populations (Seed Orchards)
Mild selection of frontier trees
(MOLP)
1st Generation Breeding Pop'n
Strong selection for specific objectives
1st Generation Seed Orchards
(MOLP filter of matings)
Control-Pollinated Progeny Test
Rogue on progeny info
Mild select. of frontier trees
(MOLP)
2nd Generation Breeding Pop'n
Strong selection for specific objectives
2nd Generation Seed Orchards
(MOLP filter of matings)
Control-Pollinated Progeny Test
Rogue on progeny info
Mild select. of frontier trees
(MOLP)
3rd Generation Breeding Pop'n
Strong selection for specific objectives
3rd Generation Seed Orchards
etc.

Figure 1. Schematic model of the proposed recurrent selection breeding strategy utilizing multiple objective linear programming (MOLP).



(a) The candidate trees in trait space

(b) The convex hull of the candidate trees



(c) The expected F_1 frontier

● = Original parent

- - -= Range in progeny values

——— = F_1 frontier

(d) Selection index with equal weights for each trait and a cutoff value of 10. Trees 4 and 9 would be selected for the production seed orchard, where the objective is max. traits 1 & 2.

Figure 2. Simple two-dimensional representation of the MOLP-directed selection procedure for a multiple-objective breeding program.

simultaneously. However, each producer can provide the breeder with his own specific objective (traits to be maximized, and weights) for the current generation of breeding. The breeder can then develop a selection index, identify the breeding individuals on the frontier for that objective (Figure 2d), and release vegetative propagules of these individuals to the producer for his commercial seed orchard.

Mathematical Statement of MOLP Procedures

The MOLP procedures for the breeding strategy can be stated mathematically as follows. First, consider J measurable traits which define the genotype (phenotype) of a set of I candidates (or families) for a breeding program. Suppose that each trait is defined such that a higher value is preferable to a lower value of that trait. There are many well known variable transformations to accomodate this feature.

Let: X_{ij} = the observed value of trait j

for candidate i, $i = 1, \ldots, I$, $j = 1, \ldots, J$.

$$X_i = (X_{i1}, X_{i2}, \ldots, X_{iJ})'$$

where X_i is a column vector, as indicated by the transpose (').

$X \subset E^J$ be the convex hull of $\{X_i, i = 1, \ldots, I\}$,

meaning that X is contained in E^J, where E^J is J dimensional Euclidean space, and

$$\text{Int } X \neq \emptyset,$$

indicating that the interior of X is not empty.

Note that certain of the I individuals correspond to vertices of X.

The first step in the procedure is to express the polytope X as the intersection of a finite number of inequalities, i.e., $X = \{x \mid Ax \leq b\}$ where

A is an M x J real matrix, and

b is a real M vector.

To accomplish this let

$$\bar{X}_j = \sum_i X_{ij}/I, \quad j = 1, \ldots, J$$

$$\sigma_j^2 = \Sigma(X_{ij} - \bar{X}_j)^2/I, \quad j = 1, \ldots, J.$$

Define the transformation $y = T(x)$ as

$$y_{ij} = (X_{ij} - \bar{X}_j)/\sigma_j \quad , \; i = 1, \ldots, I.$$
$$j = 1, \ldots, J.$$

Consider the following system defining P.

$$P = \{ p \mid \sum_{j}^{J} y_{ij} \, p_j \leq 1, \; i=1, \ldots, I\}$$

P is a polytope whose interior contains the origin. Therefore, an inclusion reversing map is established between P and its polar dual P* (Grunbaum 1967).

$$P^* = \{ p^* \mid \sum_{j=1}^{J} v_{mj} \, p^*_j \leq 1, \; m=1, \ldots, M \},$$

where v_{mj} are the components of the M vertices of P. A survey of algorithms for finding all vertices of a polytope may be found in Mattheiss and Rubin (1980).

Now let P* = T(x) to obtain the inequalities defining X.

$$P^* = T(x) = \{ T(x) \mid \sum_{j=1}^{J} v_{mj} T(X)_j) \leq 1, \; m=1, \ldots, M\}$$

So,

$$\sum_{j=1}^{J} \frac{v_{mj}}{j} X \leq 1 + \sum_{j=1}^{J} \frac{v_{mj} \bar{X}_j}{\sigma_j}, \quad m=1, \ldots, M$$

or simply

$$Ax \leq b.$$

Now that X is defined by a system of linear inequalities whose extreme points correspond to certain individuals who are candidates for the breeding program, X may serve as the feasible region for the following multiple objective linear program (MOLP).

$$\underset{x \, \varepsilon X}{\text{Maximize}} \; Cx$$

where: $X = \{x \mid Ax \leq b\}$, as obtained above, C is a K x J real matrix.

Cx is a set of K linear functionals which are to be maximized. The solution to the MOLP is a set of nondominated extreme points or efficient points E, corresponding to candidates who should be selected to participate in the breeding program. Techniques for the solution of the MOLP are given in Zeleny (1982), which contains an excellent 36 page list of references.

There are two primary constructs which may be used to specify a row of C. The first is the notion of the selection index. Each of the J traits of interest may be given a weight based on economic, heritability, genetic correlations or other arbitrary considerations. Several different selection indices may be constructed and considered simultaneously. The second notion is based on the idea of breeding all individuals who are undominated on one or more, or a combination of traits. In this case the matrix C would be a J dimensional identity matrix, since all traits are positively oriented.

Given X, a specific C will yield a set of individuals E which should participate in the breeding program. For every choice C, some set E results.

Let candidates i and ℓ be members of E. The breeding program should comprise all pairs of candidates lying on a maximally efficient face of E, for every maximally efficient face of E. Let this set of candidate crosses be called S.

$$S = \{(X_i, X_\ell) \mid X_i, X_\ell \in F_{ME}\}, \text{ for all } F_{ME},$$

where F_{ME} is a maximally efficient face of X. It may be desirable to filter S on the basis of inbreeding coefficient, breeding population size, ancestor, distance, managerial considerations, or other criteria. That is, some subset of S may be obtained for the implementation of the actual breeding program, based on several heuristics (Steuer 1980).

DISCUSSION

The MOLP procedure can be applied to either phenotypic or genotypic selection. Because of the long generation interval for most forest trees, however, we feel that phenotypic (mass) selection in the first generation and combined selection (family selection plus phenotypic selection within families) in progeny tests for later generations will continue to be used. Therefore, phenotypic values (or phenotypic scores on a comparison-tree basis) for each of 10 to 15 traits would be mapped for each tree (Figure 2a) in the first generation. A score based on family performance and individual phenotype, and weighted by family and individual heritabilities, would be used for each trait of each tree in the advanced-generation progeny tests. Genetic gains for single objectives could be calculated by standard methods, where the direction of gain is specified. Measurement of multiple-objective gain is a difficult and unresolved question, since there are an infinite number of starting points and directions which may be chosen. The distance between the frontiers of two successive generations might be used as an omnibus measure of genetic change in the total breeding program.

Inbreeding may or may not be allowed in the breeding program, depending on decision criteria made at any time and programmed into filter software. A necessary requisite will be the maintenance of pedigrees on all individuals in the breeding population and calculation of inbreeding coefficients that would occur for each candidate cross. Those crosses which would provide inbreeding coefficients above a designated cutoff level would not be made. If inbreeding reaches unacceptable levels and can no longer be constrained by this filter process, alternative methods for alleviating the problem include (i) enrichment with new selections or (ii) maintenance and crossing among subline populations.

As the number of traits and the number of trees in the breeding population increase, the number of crosses in the breeding program becomes combinatorially explosive. However, many trees that would be included in crosses in present breeding programs will not be used, since they are interior to the convex hull. Thus, the numbers of required crosses could still be less for the MOLP process than for other programs. Furthermore, filtering procedures based on heuristics such as inbreeding coefficients, mathematical "distance" between individuals on the convex hull, and number of crosses allowed per individual can be used to reduce the number of crosses to manageable proportions.

An added benefit of the MOLP-directed breeding program will be better conservation of gene resources than would occur in single-objective programs. Schoenike (1975) has listed breeding programs and their associated progeny tests as one method of gene conservation for forest gene pools. The increased number of trait combinations maintained in the MOLP program will greatly enhance the probability of conserving a broad-based sample of the natural gene pool.

APPLICATION

Current tree breeding programs can be quickly converted to the MOLP strategy by (i) combining the separate company, state, and federal programs for a particular breeding region (a provenance, or geographic race where all the trees are compatible in flower timing) into one multiple-objective program, (ii) mapping the many existing selections from this breeding region into the multiple-trait space for an expanded number of traits, (iii) identifying candidate trees on the efficient frontier to include in the MOLP breeding population, and (iv) starting the MOLP-identified controlled crosses. The university-industrial cooperatives in the southern U.S. would be logical first choices for such a strategy, since the university in each cooperative is already set up to provide the centralized administration of the breeding program. The breeding population would be maintained and managed by the university at a centralized location(s).

One advantage of a centralized multiple-objective tree breeding program for a given species in a particular breeding region would be greater efficiency in administration and costs than for many small programs. The various organizations contributing to the breeding-region MOLP program could specify their particular objectives for each generation, and the breeders would be able to identify and release to them the most genetically-advanced candidate trees for the specific objective. Vegetative propagules from these candidates can then be propagated in clonal production seed orchards at each organization's site. This procedure would allow flexibility for producers to change objectives at any time in the history of the breeding program.

CONCLUSION

MOLP procedures have been employed in water resource management and in multiple-use forestry applications. The concept represents a developed technique for addressing multiple criteria decision problems. Genetic selection is essentially a multiple criteria decision problem calling for the best available management approach. To use single objective techniques on a multiple criteria problem is to sacrifice potential gain in several traits to the attainment of one objective, which often will not withstand the test of time.

LITERATURE CITED

Franklin, E. Carlyle. 1975. Strategies for genetic gains in advanced generations of forest tree breeding. In: Forest Tree Improvement --The Third Decade. Bart A. Thielges (ed.). Division of Cont. Ed., Louisiana State Univ., Baton Rouge. pp. 147-160.

Grunbaum, B. 1967. Convex Polytopes. John Wiley & Sons, New York. 550 p.

Hazel, L. N., and J. L. Lush. 1942. The efficiency of three methods of selection. Jour. of Heredity 33:393-399.

Kung, Fan H., Calvin F. Bey, and T. H. Mattheiss. 1975. From progeny testing to seed orchard through mathematical programming. In: 13th Southern Forest Tree Improvement Conference. Sponsored Pub. No. 35, Southern Forest Tree Improvement Comm., Raleigh, NC. pp. 242-249.

Mattheiss, T. H., and D. S. Rubin. 1980. A survey and comparison of methods for finding all vertices of convex polyhedral sets. Mathematics of Operations Research 5(2).

Namkoong, G. 1970. The problem of optimality in multiple trait breeding. FAO Second World Consultation on Forest Tree Breeding. FAO. Rome. Vol. 2:775-781.

Namkoong, G. 1976. A multiple-index selection strategy. Silvae Genetica 25(5-6):199-201.

Schoenike, Roland E. 1975. Tree improvement and the conservation of gene resources. In: Forest Tree Improvement--The Third Decade. Bart A. Thielges (ed.). Division of Cont. Ed., Louisiana State Univ., Baton Rouge. pp. 119-140.

Steuer, R. E. 1980. Operating manual for the ADBASE package for solving multiple objective linear programming problems: Release 8/80. College of Business and Economics, Univ. of Kentucky, No. BA 7. 66 p.

Talbert, J. T. 1979. An advanced-generation breeding plan for the N.C. State University-industry pine tree improvement cooperative. Silvae Genetica 28(2-3):72-75.

Zeleny, M. 1982. Multiple Criteria Decision Making. McGraw-Hill Book Co., New York. 563 p.

PORGENY TESTING METHODOLOGY

LESSONS FROM ONE GENERATION OF PROGENY TESTING
OR
ROBERTS RULES OF DISORDER*

by

Robert J. Weir, J. P. van Buijtenen and R. E. Goddard**

The authors have worked many years with large progeny testing programs and have accumulated a half-vast storehouse of knowledge concerning ways to wreck progeny tests plots beyond salvage. It is our sincere intent to share this valuable experience with you. We elected to summarize our experience in the form of recommendations. The researcher then needs only to decide the type of catastrophe desired in his or her progeny tests, locate the appropriate procedure (e.g. 2a, 3b, etc.) and instruct research technicians accordingly. It is hoped that in this way this document will serve as a foolproof guide to guaranteed disaster.

1. Design and Scheduling

a) Don't think too much about statistical design and analysis until the study has been established. Things never go exactly as planned anyway, and it is much better to take your data to a statistician after you have collected them. A good statistician armed with a modern computer can analyze anything.

b) An efficient researcher plans work well in advance and sticks to the schedule. If your schedule is to plant a progeny test on December 16, the lack of any rain since September 2 is a minor circumstance and no reason to alter the schedule. Never in any case resort to an alternative to the original plan.

c) If a and and b appear contradictory, they are! So what.

2. Nursery Phase - This has very little to do with progeny testing, don't bother with minor details.

a) Variable bed density has little effect on anything, you can always cull the runts at lifting time.

b) Do not leave space or use dividers between seedlots, bed space is too valuable. Besides, undercutting hardly ever mixes lots and genetic differences allow you to sort them out if it does.

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*These thoughts were first presented in: Progeny Testing of Forest Trees. Southern Cooperative Series Bulletin 275. Texas A & M University, College Station, Texas 77843. February, 1983. pp. 24-26.

**The authors wish to recognize numerous irrelevant contributions by William J. Lowe, Director of WGTIP.

c) If the nursery crew slips up and lifts and sells your progeny test seedlings to private landowners, it is O.K. You may need a very large map on which to locate all plantings, but the extra precision gained from planting seedlings in many locations makes the trouble worthwhile.

d) When lifting, counting and sorting seedlings prior to planting, just get the job done. A bit of extra root drying is not too serious, and it is bothersome to keep them protected at all times.

e) When preparing to plant your test (lifting, sorting, etc.), do not despair if certain families are minus a few trees. Simply choose enough to balance the test from families that have extra. Be sure to select these extra seedlings in a random manner to maintain the integrity of your statistical analysis.

3. Layout and Planting

a) Lay out a progeny test as much as possible in a perfectly square block to conserve space.

b) In order to further conserve space be sure to plant through areas formerly occupied by windrows. Depending on the sophistication of the experiment one has the following options:

1) Ignore windrows altogether.

2) Plant the rows perpendicular to the windrows, while the rep stradles the windrow.

3) Plant the rows parallel to the windrows, with the replications at right angles to the windrow.

4) Arrange reps as well as rows at 45° angles with the windrows.

c) In hilly terrain always orient the family rows parallel to the contours to preserve uniformity within plots, unless, of course, it interferes with maintaining a perfectly square layout.

d) Never plant a test in the path of an ice storm, tornado, hurricane or flood. To locate the desired "safe" areas for testing, consultation with the Almighty is required. Your local weatherman or Corps of Engineers Officer can make these contacts for you.

e) It is not a problem to plant trees next to train tracks, particularly if unscheduled control burns are periodically desired. Trains have on occasion wrecked and trees close to the track have been prematurely sheared. Out of control freight cars rolling through progeny tests are known to leave very high stumps which are a problem.

f) Be sure to plant the trees at exactly regular spacings. It is better to put trees in potholes or in stumps than to disrupt the spacing. If there is water in the pothole be sure that at least a tiny bud sticks up above the water.

g) The person who establishes a progeny test will always be the one to measure the test. Therefore, detailed notes and establishment reports are not necessary. Don't bother with a North arrow or date on the map. Marking position and number of borderrows is also superfluous. After all the bloody work you did planting the test you will remember those details forever.

h) Randomization within replications is a time consuming process and can be made optional depending on the planter. If a randomization plan must be used, remember Super Seedlings are extra tough so it is O.K. to lay the bundles out in the sun while you are trying to figure out where in the hell they go.

i) Plant trees on fresh clearcuts when possible. Pales Weevil is a figment of the imagination.

4. Maintenance

a) Progeny tests need mowing the first few years, but it is best to do this when there is no other job pressing for your attention.

b) The best time to mow the first year is August. The weeds may be a bit taller than the trees, but after mowing once, the rows that are left will be much easier to see.

c) Leave some hardwood sprouts near each tree to give them some shade and help mark the rows when the trees are small.

d) If you want to cut down on mowing, progeny tests are an ideal place to experiment with herbicides. Be sure to put out enough. Too little will give no control and just waste your time.

e) Be sure to put firebreaks around your tests, but leave an opening for your car to get through.

f) Detailed instructions to tractor operators are not necessary. When told to mow a progeny test, they probably will!

g) First year mortality can be easily handled by replanting at any time during the first five years of the test.

h) If tags are needed be sure to snug wires tightly around test seedlings. Girdling of tagged trees will slow growth only slightly and promote early pollen production. If tag wires are not tightly wrapped they may be lost.

i) Designate areas within tests for cattle to graze. They will destroy only a few trees and reduce mowing costs substantially.

j) Erect signs around the perimeter of all test plots reading as follows: Beavers, Deer and Pulpwooders Keep Out!! Since all of these pests can follow instructions equally well, the instructions are certain to be heeded.

5. Measurements

a) When taking measurements be sure to use your map for orientation. If the tags don't agree with the map, the map takes precedence. Not checking the tags saves much confusion and time.

b) Don't bother to write down location, date and measurement units. Even if you don't remember you will be able to tell from the plot layout and magnitude of the numbers.

c) There is no need to always measure a row the same way or use a fixed convention in measuring block plots. You can always match new measurements with old measurements by checking where the missing trees are located. Besides, there are only two ways to measure a row plot and sixteen ways to measure a block plot.

d) Diameter measurements should always be made at DBH regardless of branch whorls forking or fusiform rust galls to avoid biasing data.

e) When measuring tests, speed is the most important thing to concentrate on. If haste causes some measurement error, don't worry, every Analysis of Variance needs an estimate of error for use in significance testing. Transformations can often be useful if Error is too large.

Good luck with your own personal catastrophes!

PROGENY TEST DESIGN AND ANALYSIS

J. P. van Buijtenen[1]

Abstract.--A workshop on progeny testing was held in Auburn, Alabama on June 15-16, 1982, sponsored by Cooperative Regional Project S-23, "Breeding Strategies for Genetic Improvement of Commercial Forest Trees in the South".

Topics covered were objectives of progeny tests; mating designs; raising progeny test seedlings; field designs; test establishment, maintenance, and measurement; and data handling and analysis.

This paper summarizes parts of the workshop, particularly the topics related to the design and analysis of progeny tests. Emphasis is placed on the practical rather than theoretical aspects, although both were covered in the workshop.

Copies of the proceedings can be obtained from any of the cooperating state agricultural experiment stations.

Additional keywords: Polycross, diallel, factorial design, nested design, field layout, data handling.

INTRODUCTION

The following paper is a summary of the highlights of the S-23 Workshop on progeny testing held in Auburn on June 15-16, 1982, emphasizing the design and analysis aspects. It will touch on mating designs, field layout, and the management and analysis of progeny test data. The choice of designs depends to a large extent on the objectives and the overall breeding strategy of the particular tree improvement program involved. As pointed out by McKinley (1983), the most common objectives of progeny tests are: a) to provide information for evaluating parents; b) to estimate genetic parameters; c) to produce a base population for advanced generation selection; and d) to estimate realized gain directly.

Since it is not always possible to meet the progeny test objectives with a single progeny test, it is often necessary to assign priorities. Such priorities are sometimes difficult to identify and may depend on the goals of the organization involved, the timing of the progeny test and the generation one is working on. In the inception of a breeding program, delineation of seed sources may rank very high, while at a later stage advanced generation breeding may be the primary goal.

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MATING DESIGNS

There is a large variety of mating designs. They can be divided into two main groups, single designs and complementary designs. Since in a practical breeding program, one usually tries to achieve several objectives at once, any single design may be reasonably useful for all purposes, but not necessarily the best for any one of them. The concept of complementary designs is based on the philosophy that it can be an advantage to combine several simple designs, each of which is very efficient for one particular purpose.

Open-Pollinated Designs

Open-pollinated progeny tests may be obtained from ortets as they occur in the woods or ramets in seed orchards. Selections from open-pollinated progeny tests obtained from seed orchards may be related, and crosses among them may involve inbreeding and all the problems involved with inbreeding depression. Using open-pollinated seed from ortets in the woods avoids this problem, but one loses the gain associated with selection of the male parent. Open-pollinated tests are useful to evaluate parents if the pollen is a good mixture and does not vary much from tree to tree, but may be unreliable if each female parent has a unique and different pollen sample. The experience of several organizations indicates that there may indeed be a problem, since the results of open-pollinated tests do not always agree with those of subsequently obtained control-pollinated tests. Open-pollinated tests of seed obtained out of a seed orchard would seem a very appropriate means of determining realized gain in that particular orchard.

The Polycross

The polycross design is in many ways similar to the open-pollinated test. A set of pollens is mixed and used to make control pollinations. Polycross tests are very good for determining general combining ability and, thus, for evaluating parents, but generally are not suitable for making advanced generation selections, since inbreeding may result because of relatedness between the offspring. Several interesting modifications of the polycross are discussed by van Buijtenen and Namkoong (1983).

The Complete Diallel

The complete diallel consists of all possible crosses among the available parents. This design obviously will give the maximum amount of information possible on the parents included in the test. The number of crosses, however, goes up as the square of the number of parents and the cost and time required very quickly become unmanageable. For an orchard including 40 clones, it would, e.g., take 1,600 crosses to make a complete diallel.

The Modified Half-Diallel

This is similar to the complete diallel, but omits the selfs and the reciprocal crosses. Although the number of crosses is somewhat less than half of that of the complete diallel, it is still quite large. Although it is still possible to estimate both gca and sca, it is no longer possible to study the effect of selfing and of making reciprocal crosses.

The Disconnected Half-Diallel

This is a variant of the modified half-diallel created by dividing the parents into equal sets and making a modified half-diallel within each set. A disconnected six-tree half-diallel, e.g., would involve 15 crosses per set. This kind of design is a reasonably good compromise that allows one to determine gca and sca. It is good not only for evaluating parents, but also for identifying outstanding specific crosses. It also is quite useful as a means of generating a population in which to make selections for the next generation. There is a problem, however, in that usually not all disconnected diallels can be planted in one field test, which means that one cannot capture the genetic variation between the sets. Particularly in small sets this can be a substantial amount since van Buijtenen and Burdon (1983) found that the amount of additive genetic variation between sets is equal to the total additive genetic variation divided by the number of parents. In the six-tree disconnected diallels this would leave, for instance, 1/6 of the additive genetic variation between the sets.

Partial Diallels

In a sense, any set of crosses short of a complete diallel could be called a partial diallel. However, one usually refers to a design consisting of one or more sets of crosses following the diagonals across the diallel tables. This again is a fairly good compromise that allows one to evaluate parents, estimate genetic parameters, and make selections for the next generation.

Factorial Designs

In a factorial design, two separate groups of parents are crossed with each other in all possible combinations. In the disconnected factorial, the same principle is followed as in the disconnected diallel: the population is sub-divided into groups and the trees within each group are crossed according to a factorial design. Pepper and Namkoong (1978) made a detail economic evaluation of both nested and factorial designs for progeny testing. The factorial design is generally slightly superior to the nested design in terms of evaluating parents. For evaluating genetic parameters, the factorial is usually not quite as efficient as the various diallel designs. For selection of new parents for the next generation, the factorial design can be quite satisfactory if there are enough male parents. The four tester design employed formerly was not very well suited, because of the high degree of relatedness among second generation selections which resulted from this design.

Nested Design

In a nested design, one parent is crossed with a number of other parents. Usually the male is the rare parent which is crossed with several females. Each female, however, is crossed with only one male. The nested design is not too efficient for many purposes, such as evaluating parents and estimating genetic parameters. It could, however, work very well in a complementary design where family selection is handled with a design such as a polycross, while the nested design provides a source of trees for the following generation. This would be particularly true if some of the parents are known already, in which case the best general combiners could be assigned to the rare parent.

FIELD DESIGNS

Field designs were discussed by Bridgwater et al. (1983). The basic rule is again that the field design needs to be appropriate for the particular objective being served. In an operational tree improvement program, quite often a compromise needs to be struck between a number of practical considerations and the needs of the various objectives to be accomplished. From the practitioner's point of view, the question to be answered is a very simple one: Where do I plant each tree? This is about where the simplicity ends. Borrowing a concept from computer science, we can take the top-down or bottom-up approach in discussing this problem and I'd like to follow the top-down approach.

How Many Locations are Needed?

Philosophies in this respect seem to differ widely by region. In the South, the common procedure is to plant the same families on three or four different locations. In some western programs, families may be planted in 12 to 16 locations. Which is the better approach depends on the type of tree one wants to select and on the amount of genotype x environment interaction that is present.

Let's start by looking at the genotype x environment interaction. If no genotype x environment interaction is present, in other words if all families rank the same on all sites, one needs to test on only one site. If genotype x environment interaction is present, however, one needs to make a decision. One can either select a general purpose tree that may not grow the best at any given location, but will grow reasonably well at almost all locations, or one can select genotypes that are specifically adapted to a given site. This will greatly influence the strategy of the testing.

If one wants to select for a generally adaptable type, one could plant relatively small numbers of trees per family in a given location and plant the families on many locations. This should give one the best possible evaluation, although one would have only very limited information on the suitability of a particular family for a given site.

If one wants to know something about the adaptability to a specific site, one needs to increase the number of trees per family planted at a given location. Economics, as a consequence, will force a reduction in number of test sites to keep the cost of progeny testing within reason.

Although I never heard anybody address this issue, I feel that the western tree improvement programs lean towards the general adaptability approach, while the southern programs are somewhat of a compromise evaluating general adaptability, but also obtaining some information on the performance of a family at a given site.

How Large Should a Test Be at a Given Location?

This is really not a meaningful question, since the size of the test itself is not critical. It is the size of a single replication that is critical.

To maintain soil uniformity within a replication, it is necessary to keep the replication size as small as possible, about 1/4 to 1/2 acre maximum. There is no definite limit to the number of replications one could include. The number of replications needed depends on the precision desired and the plot size, which will be discussed later. A typical test includes about 2,000 trees, although I've seen tests of less than 500 trees and tests of around 10,000 trees.

How Many Families Should Be Included in a Test?

This again is closely tied to the size of the replications and the size of the plots. If we assume that the maximum replication size is about 1/4 acre and the spacing is 8 x 8 feet, then the relation between plot size and the maximum number of families included in a test is as depicted in Figure 1. For a 1/2 acre replication and 10-tree plots, this would amount to about 34 families. Using single tree plots, one could accomodate well over 100 families and keep the replications smaller than 1/2 acre.

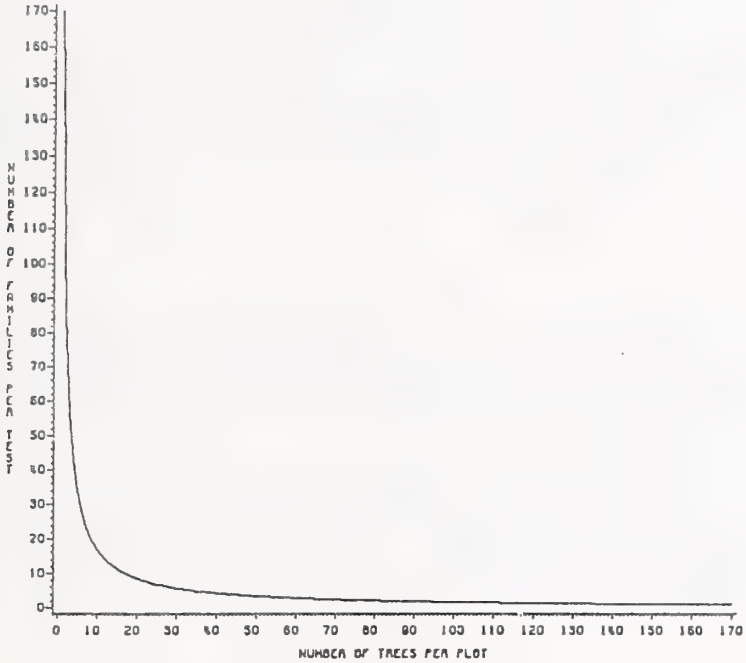

Figure 1. Relation between plot size and number of families per test, assuming a replication size of 1/4 acre and a spacing of 8 x 8 feet.

How Many Replications Per Location are Needed?

Again this question cannot be answered categorically, it depends on the precision desired and the plot size. There are sophisticated statistical formulae available to calculate this, but in practice the total number of trees needed per family remains relatively constant and is mainly distributed differently between replications and number of trees per plot. This is not quite true, however. Although one needs more replications with smaller plots, the total number of trees needed is somewhat less. In general, smaller plots and more replications will give greater precision. In our experience, six replications and four trees per plot are definitely not enough, while ten replications of 10-tree row plots are probably more than needed.

How Many Trees Per Plot are Needed?

This has been largely covered under previous headings, but a few things remain to be said. Over the last 30 years, experiments have been put in, which range from large 100-tree plots to single-tree plots. From a statistical point of view, the single-tree plots and a modification often called non-contiguous plots offer the greatest advantages. However, they are very difficult to establish and maintain. Hundred-tree plots are too large, since one could include only about six families in a 1/2 acre replication. As a consequence, there usually is a large family by replication interaction making it very difficult to distinguish between the performance of individual families. Small row-plots utilizing anywhere from 4 to 10 trees per plot currently seem to be most common. They allow a reasonable number of families per test, are easy to handle in the field, and give good statistical precision if a sufficient number of replications is used. They also lend themselves well to making second generation selections, as selected trees can be compared to the other trees within the same plot. Single-tree plots are very difficult to use for second generation selections, since members of the same families are scattered throughout a replication. We are currently looking at different ways of evaluating single-tree plots and non-contiguous plots, but a satisfactory solution has not been found yet.

Laying Out the Test in the Field

This is by far the most critical and most difficult phase of progeny test design. There is no such thing as a perfectly uniform piece of land and care must be taken to properly cope with the different kinds of site variability encountered. Following are some examples of site variability and what to do about it.

1) Slope.--The common way to reduce the impact of slope on the evaluation of the families is to lay out the replications parallel to the contour lines and the rows perpendicular. This way there may be some increased variability within the plots, but each family will sample roughly the same type of environment.

2) Pimple mounds, small depressions, and potholes.--Two approaches are possible here. If the area is too large, it is best not to include it in the test. This may cause the replications to be separated from each other, however, this is far preferable over including the soil variation. If the unusable areas are small, a common approach is to plant filler trees. These serve to reduce border effects and are not included in the measurements.

3) Distinct changes in soil type.--Try to keep one replication in the same soil type, thus, avoiding a change in soil type in the middle of one replication. Again, this may cause one replication to be separated or off-set from the others.

PROGENY TEST DATA HANDLING AND ANALYSIS

This was discussed in considerable detail at the S-23 meeting (Lowe *et al.* 1983), including the statistical aspects, but I will mostly highlight some of the practical aspects.

Data Collection

The most common way to do this is probably still by handwriting the numbers either on special forms or on 80-column computer coding forms. Regardless of the system used, it is nice to have the previous measurement available on the form to help identify position in the field, to record recent mortality, and use old measurements for confirming the validity of the new ones.

Recently new equipment has been introduced where measurements can be keyed immediately into an electronic recording device. In principle, it is possible to use a wand-like device to record tree identification just like it is done in grocery stores. Labels, however, are subjected to a lot of dirt, wear and tear in the field, and this approach has not turned out too well. The recording devices themselves, however, have been quite satisfactory, and a number of them are in use. Data can be transmitted over a telephone line to the main computer after which data can be edited and stored. It is also possible to load a file of previous measurements into the recording device which can be displayed while new data are recorded, giving the same advantages as recording new data along with previous measurements on paper. This field is developing so rapidly that before very long there will be several cheap and sophiscated devices on the market that will make a complete shift to automated data recording almost unavoidable.

Data Editing

In addition to proofreading, it is advantageous to run the data through an editing program that will flag potential errors. This can be done, for instance, by having it compare new measurements to previous measurements, and by specifying ranges within which the data are expected to fall. Another way to flag potential errors is to calculate standard deviations for each plot and double check the plots with unusually large standard deviations. Other items that the editing program should check are the genetic identification codes, the number of replications, and the number of observations within each replication.

Data Storage and Backup

The data are usually stored on cards, tape, discs, or diskettes. It is absolutely essential to have some form of backup. In other words if the data are on tape, they should be on two separate tapes kept in two separate locations, or if the data is stored on a disc or diskette, they should be backed up by tape or loaded on a separate disk. Data stored on electro-magnetic devices are particularly vulnerable to complete or partial loss due to computer failures. In addition, it is a good idea to have a paper backup such as a recording sheet or a printout.

Statistical Considerations

There is no need to go into detail on the statistical aspects, but I would like to relate some of the major areas that were covered at the meeting. A major portion was devoted to the analysis of single location tests. This is relatively straightforward if one has a well-balanced set of data in hand. These seem to be a rarity, however. Fortunately, a number of computer programs are available that handle unbalanced data relatively well, although some loss of precision usually occurs.

A much more difficult problem is the analysis of tests planted across multiple locations. Inevitably some families will rank differently on one location than on a second location. This could be due either to inaccuracies in the progeny test or because a particular family may be better adapted to one site than the other. As discussed earlier, at this point one needs to decide whether one wants to select for a family adapted to a particular site or for families that are adaptable to a range of sites. Regardless of the decision, one will have to determine how a given family responds to a range of site qualities. This can be done fairly readily using a regression approach as is illustrated in Figures 2 and 3. Some well-known seed sources are good examples of these type of responses. Livingston Parish loblolly pine, for instance, has a rather steep response curve, indicating it does relatively poorly on low site index land, but does extremely well where the site index is high. By contrast, the drought hardy sources from the Lost Pines area in Texas have a relatively flat response and do reasonably well on poor sites, but do not increase their growth as much as Livingston Parish when planted on good sites.

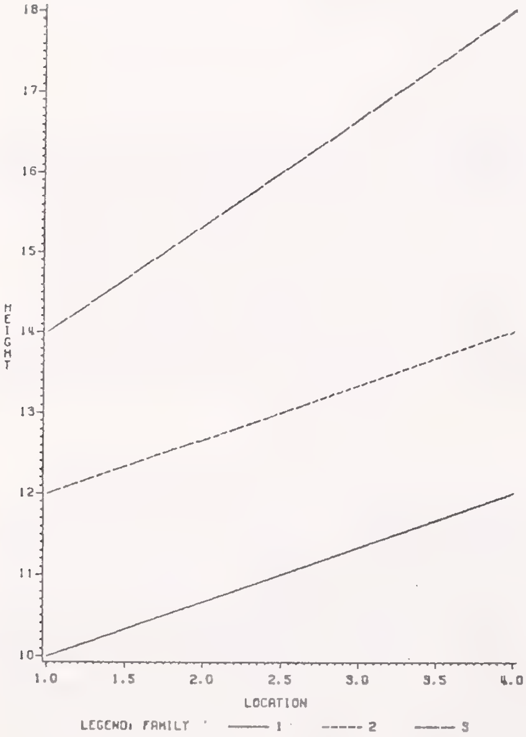

Figure 2. A genotype x environment interaction caused by an increase in variance among families on better sites.

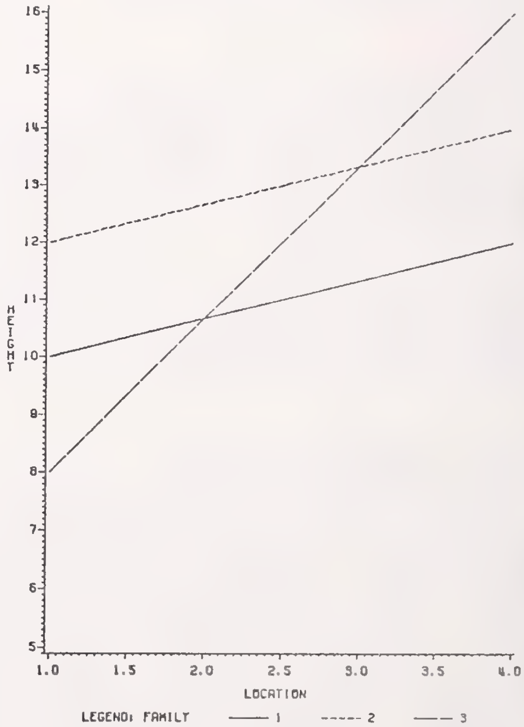

Figure 3. A genotype x environment interaction caused by a change in family rank at different locations.

Data Summarization Across Tests

This is an extension of the problem discussed in the previous section, except here the purpose is to rank families for roguing a seed orchard. Several major problems need solving. The data are usually unbalanced and the trees are planted over a range of sites. To put the data on a common basis, the family averages at a given location need to be expressed in a way that is independent of site. This can be done by expressing them as a percentage of the checks. This does not always work too satisfactorily because different tests may have different checks included, or they may have so few checks that the check doesn't form a stable base line. Commonly it does work well to express a family as the percent of the average of the progeny test. This in itself can create problems, because some progeny tests may be composed of better genetic material than others. Another good approach is to express the ranking of a family in terms of standard deviations. The N.C. State performance index is based on this principle (Hatcher et al. 1981).

A system that, as far as I know, has not been implemented anywhere, but which theoretically looks the best is to weight family averages by plantation according to their standard errors. In other words, the more reliable the observation, the higher weight it will carry. These weighted averages are then fitted across progeny test sites using a least squares procedure. This gets very demanding in terms of the amount of computer memory required, and the data needs to be complete enough where the values of the families can be properly estimated. No system is totally satisfactory yet, but good progress has been made.

CONCLUSIONS

The mating design and progeny test design need to be matched to the progeny test objectives. One has the choice between some reasonable compromise solutions and a complementary design consisting of a combination of single tests, each serving a specific objective.

A revolution in data collection is underway with the advent of electronic data recording devices. As fast as this field is developing, it seems likely that the clipboard and notepad may suffer the same fate as the slide rule.

Satisfactory means of analyzing each type of design are available, including programs that will handle unbalanced data. Several workable systems of summarizing data across tests are available, but there is a need for further improvements in technology in this area.

LITERATURE CITED

Bridgwater, F. E., J. T. Talbert, and D. L. Rockwood. 1983. Field Design for Genetic Tests of Forest Trees. In Progeny Testing of Forest Trees, Proc. of S-23 Workshop on Progeny Testing, June 15-16, 1982, Auburn, Alabama, Southern Cooperative Series Bulletin No. 275, pp. 28-38.

Hatcher, A. V., F. E. Bridgwater, and R. J. Weir. 1981. Performance Level -- Standardized Score for Progeny Test Performance. Silvae Genetica 30(6): 184-187.

Lowe, W. J., R. Stonecypher, and A. V. Hatcher. 1983. Progeny Test Data Handling and Analysis. In Progeny Testing of Forest Trees, Proc. of S-23 Workshop on Progeny Testing, June 15-16, 1982, Auburn, Alabama, Southern Cooperative Series Bulletin No. 275, pp. 51-67.

McKinley, C. R. 1983. Objectives of Progeny Tests. In Progeny Testing of Forest Trees, Proc. of S-23 Workshop on Progeny Testing, June 15-16, 1982, Auburn, Alabama, Southern Cooperative Series Bulletin No. 275, pp. 2-5.

Pepper, W. D. and G. Namkoong. 1978. Comparing efficiency of balanced mating Designs for Progeny Testing. Silvae Genetica 27(3-4):161-169.

van Buijtenen, J. P. and G. Namkoong. 1983. Mating Designs. In Progeny Testing of Forest Trees, Proc. of S-23 Workshop on Progeny Testing, June 15-16, 1982, Auburn, Alabama, Southern Cooperative Series Bulletin No. 275, pp. 7-13.

van Buijtenen, J. P. and R. D. Burdon. 1983. Efficiency of Mating Designs for Second Generation Selection. (In Preparation).

Use of a Lattice Square Design to Evaluate Family Effects: Accounting for Environmental Variation

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Abstract. A loblolly pine (Pinus taeda L.) open-pollinated progeny test consisting of 43 families and 6 checks was designed as a 7 X 7 lattice square to determine the value of the lattice as an aid for the evaluation of parental genotypes. The precisions of the lattice for height variables, when compared with a randomized complete block analysis (RCB), ranged from 100 to 107 percent after the first year and 100 to 110 percent after the second year. For the variable tipmoth damage precisions of the lattice were 178 and 199 percent. The lattice analysis accounted for more environmental variation than did the RCB analysis. Adjusted means generally agreed with unadjusted means but over 95 percent were altered and in all cases the rankings were changed. The preciseness of the lattice analysis gave confidence that families were evaluated accurately.

Additional keywords: Pinus taeda L., height increment, increase in precision, family evaluation, adjusted means, experimental design.

A primary function of progeny testing is the evaluation of parental genotypes (McKinley 1983). These evaluations serve many purposes in a tree breeding program. Successful evaluations require accurate estimations of family means (Bridgwater et al. 1983), and to obtain accurate estimations we need to account for enviornmental variation. Heterogeneity of sites and experimental size can both contribute to increases in environmental variation. The appropriate choice of a field design can aid in accounting for environmental variation and assure quality in the information obtained from the test.

A lattice design could aid in partitioning the error variance and increase the chances of correctly evaluating treatment effects. Thus, in some cases, researchers could possibly derive more information from their efforts by increasing the intensity of planning and analyzing their tests. In a provenance study of red pine, Lester and Barr (1965) found significant differences among progenies only by using the increased precision of a lattice analysis. Synder (1966) made a survey of lattice experiments and found that 12 of 17 gave rates of efficiency, where the lattice error was compared to that of the randomized complete block (RCB), of at least 110 percent, and ranged up to 275 percent. Wright (1978) indicated the usefulness of adjusting family means when obvious within-block variation was present and described a "moving average" method to do so. In the present study, a lattice analysis was used to adjust family means for genetic evaluations and the value of the lattice design was determined.

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METHODS AND MATERIALS

A loblolly pine, open-pollinated progeny test was established in the Alabama Piedmont. The 2.95-hectare, old field site had a Gwinnett sandy clay loam soil and was suspected to have both fertility and moisture gradients. The test consisted of 43 families and 6 checks designed as a 7 X 7 lattice square requiring 4 replications. Each replication had 7 rows and 7 columns, laid out according to expected gradients, for a total of 49 plots. The arrangement of plots within each replication came from a permutation of the layout presented by Cochran and Cox (1957). Each family plot consisted of four 5-tree rows for a total of 20 trees. Each plot was bisected and fertilizer was randomly assigned to one of the groups of 10 trees. Two 10-gram tablets (20-10-5) were placed in the first closing slit when planting.

Total heights were measured at the time of planting and after the first and second years in the field. Tip moth damage was not anticipated and no control measures were taken the first year. When the damage was detected and the severity scored, it was added as a variable to determine its effect on height growth and the effect of families on its occurrence. Tip moth damage did not alter height comparisons and served as an additional environmental variable for evaluation of lattice adjustments since blocking could not be depended upon to account for this variation. Control measures were performed during the second growing season. Total heights and increments were analyzed both as a randomized complete block and a lattice square. Both analyses are statistically appropriate. The format of the lattice analysis (Table 1) allowed for part of the error term to be accounted for by rows and columns which reduced the error mean square but also reduced the degrees of freedom. Treatment means were adjusted for the row and column effects and compared to unadjusted means. Variance component estimates were computed for both unadjusted and adjusted means and were compared.

RESULTS AND DISCUSSION

There was significant variability for nursery heights and heights after 1 year for these trees (Duba et al. 1982). It was determined from looking at first-year increments that the tallest families did not always have the largest increments, but their height advantage from the nursery had been retained. During the second growing season, those families that had the largest increments were able to overtake those with large nursery heights and constituted the majority of the tallest families. Therefore, height increments during the first and second years in the field, as well as total heights, were necessary to evaluate family effects.

Randomized complete block analyses. -- Since it is statistically appropriate to analyze these data as randomized complete blocks, this was done as a basis for evaluation as a lattice. There were significant differences among families for total heights and increments for all cases except the fertilized 2-year increments (Table 2). Family means could be separated and ranked for selection.

Family by fertilizer interactions were evaluated with the randomized complete block analysis and were significant for 2-year increment (α=0.02) and

Table 1. Composition of the randomized complete block and lattice square analyses of variance

	Randomized complete block		Lattice square	
	Source	df	Source	df
By Fertilizer	Replication	3	Replication	3
	Family	48	Family	48
	Rep * Family	144	Row (adj)	24
			Column (adj)	24
			Rep * Family	96
Among Fertilizer	Replication	3	Replication	3
	Family	48	Family	48
	Rep * Family	144	Row (adj)	24
	Fertilizer	1	Column (adj)	24
	Fam * Fert	48	Rep * Family	96
	Rep * Fam * Fert	147	Fertilizer: T-test (adj treat difference)	
Pooling over Fertilizer	Replication	3	Replication	3
	Family	48	Family	48
	Rep * Family	144	Row (adj)	24
			Column (adj)	24
			Rep * Family	96

second-year increment ($\alpha=0.01$). For 2-year total height, the level of significance was $\alpha=0.06$ which is not significant in a strict statistical sense, but probably is in a biological sense. Thus, to get another evaluation of the lattice, total heights were also pooled over fertilizer and examined (Table 2).

Lattice analyses. -- It has been typical of most studies attempting to determine family growth differences that the separation of means becomes easier as the test ages. This has been true for lattice analyses in forestry applications and should also be true of this test. Of the 6 lattice analyses computed for first-year height measurements, 4 gave increases in precision ranging from 103 to 107 percent while the other 2 gave 100 percent precision (Duba et al. 1982). Of the 7 lattice analyses computed for second-year height measurements, 6 gave increases in precision ranging from 101 to 110 percent while 1 gave 100 percent precision (Table 2). The 2 lattice analyses of the tip moth damage gave increases in precision of 178 and 199 percent.

Although the increases in precision indicated that the lattice accounted for more variation, there were fewer degrees of freedom associated with the effective error term of the lattice. Hence, the probability associated with the lattice F-test on family means was not necessarily smaller than that associated with the RCB analysis. An additional analysis was made to evaluate the adjustment of means by the lattice. In this case the adjusted means were reanalyzed using the RCB model. It was not known just how to adjust the error degrees of freedom to account for the adjustment of means, but Wright (1978)

TABLE 2. Characteristics of the lattice and randomized complete block analyses

Variable	Year	Increase in precision	Lattice adjustment[b/]		Coefficient of variation		Average adjustment of treatment means	PR>F		
		%	Row	Column	RCB	Lattice	%	RCB	Lattice	adjusted[c/]
Total height:										
F = 0, 1[a/]	2	106	+	+	8.9	7.8	0.8	.001	.001	.0001
F = 0	2	101	0	+	10.7	10.1	0.6	.002	.005	.0006
F = 1	2	110	+	+	10.6	8.8	1.6	.009	.005	.0001
Increment:										
F = 0	0-2	101	0	+	14.6	13.8	0.7	.022	.041	.0107
F = 1	0-2	105	+	+	15.1	13.3	1.5	.066	.109	.011
F = 0	1-2	100	0	+	14.7	14.1	0.7	.010	.024	.005
F = 1	1-2	107	+	+	14.9	12.9	1.7	.021	.047	.002
Tipmoth:										
F = 0	1	199	+	+	51.0	28.4	29.3	.06	.04	N.C.
F = 1	1	178	+	+	58.3	37.0	20.9	.68	.68	N.C.

[a/] F = 0 if not fertilized, 1 if fertilized.
[b/] 0 if not affect adjustment, + if affect adjustment.
[c/] Analysis on means adjusted by lattice, using RCB model.
N.C., not calculated.

decreased the error degrees of freedom by one when using his "moving average" adjustment. The F-test probabilities for this analysis are on the order of ten times smaller than for the other analyses (Table 2).

In the case where the lattice probability was not smaller than that for randomized complete blocks, the value of the lattice was in adjustment of treatment means for their genetic evaluation. For each variable, the lattice analysis adjusted over 95 percent of the family means and altered the ranking of families. Adjustments to family means ranged from 0.0 to 5.6 percent, with the averages for each variable ranging from 0.6 to 1.7 percent (Table 2).

The row and column adjustments of the lattice gave an indication as to the effectiveness of blocking on the expected environmental gradients. The column adjustment corresponded with the gradient expected to be most severe and, as can be seen, made an adjustment on each variable (Table 2). The row component was variable in its affect on adjustments. The value of the lattice would have been greater if the environmental gradient associated with rows had been greater. As the test continues, environmental effects may become more pronounced and both row and column effects may increase, which would result in a higher precision. On the other hand, the environmental gradient associated with rows may not become accentuated and would not have been needed in the design.

In all of the lattice analyses, the coefficient of variation for family means decreased from the randomized complete block value. This was due to rows and columns assuming some of the variation in the model. The smaller coefficient of variation indicates that differences between family means could be detected more readily. This was the case for the adjusted mean RCB analysis where the F-test probabilities were very small (Table 2).

Variance components were computed for both unadjusted and adjusted family values and compared (Table 3). In the analysis on adjusted means, the effective error increased in the percent of variability accounted for and so did families. These increases were accompanied by a decrease in the replication component of variation. Thus, the value of the lattice in adjusting treatment means is again demonstrated by increasing the contributions of families.

Table 3. Comparison of variance component values for unadjusted and adjusted treatment means for nonfertilized plots

Variable	Variance component	Percent of total RCB	Percent of total Lattice (adjusted)
Second-year height:	Rep	17	7
	Family	15	19
	Error	68	74
Two-year increment:	Rep	31	16
	Family	9	12
	Error	60	72
Second-year increment:	Rep	24	13
	Family	11	14
	Error	65	73

Adjustments of means and rankings. -- The family component for second-year total height (fertilized plots) was significant ($\alpha=0.009$) for the RCB analysis, was more significant ($\alpha=0.005$) for the lattice analysis and still more significant ($\alpha=0.0001$) for the analysis on adjusted means. The row and column components of the lattice accounted for enough additional variation to give a 110 percent precision and allow the means to be adjusted accordingly (Table 4). If a selection was being made of the top 5, 10 or 15 families, there would be 2, 2, and 4 changes, respectively, by selecting on adjusted instead of unadjusted means.

Table 4. Comparison of adjusted and unadjusted second-year heights for fertilized plots of loblolly families.

Family	RCB unadjusted height (cm)	Rank	Lattice adjusted height (cm)	Rank	Number of changes[a]
456	121.8	1	123.7	1	
56	113.9	2	110.3	6	
139	113.8	3	112.4	3	
186	113.6	4	113.8	2	
182	113.1	5	108.2	8	2
447	112.4	6	110.4	5	
138	109.1	7	106.9	14	
55	108.6	8	112.0	4	
38	108.0	9	107.6	10	
137	107.9	10	107.4	11	2
517	106.7	11	102.4	29	
453	106.6	12	106.6	16	
454	106.5	13	108.2	7	
457	106.3	14	104.6	23	
523	106.1	15	106.5	17	4

[a] Number of family differences within ranks 1-5, 1-10, and 1-15.

The family component for second-year increments (fertilized plots) was significant ($\alpha=0.021$) for the RCB analysis, was less but still significant ($\alpha=0.047$) for the lattice, and was most significant ($\alpha=0.002$) for the analysis on adjusted means. A 107 percent precision allowed for adjustment of means and rankings (Table 5). Selections would be altered for 2 families in each of the categories of top 10 and 15.

Tip moth damage was an influence that might have been expected to occur in a gradient from an area of initial or concentrated attack. Lattice analyses for this variable gave increases in precision of 178 percent for the fertilized family plots and 199 percent for the nonfertilized family plots. The adjustments to the means (Table 6) were considerable and the rankings were changed to a large extent. The probability of family differences was increased from 0.06 to 0.04 for the nonfertilized family plot analysis.

Table 5. Comparison of adjusted and unadjusted second-year increments for loblolly families from fertilized plots.

Family	RCB unadjusted height (cm)	Rank	Lattice adusted height (cm)	Rank	Number of changes[a]
456	70.7	1	71.7	1	
56	70.0	2	67.8	4	
139	69.3	3	69.5	2	
73	68.8	4	69.5	3	
447	68.3	5	66.4	5	0
182	67.7	6	64.1	7	
186	66.6	7	66.4	6	
38	63.9	8	64.0	8	
517	63.8	9	60.5	19	
137	63.0	10	62.5	12	2
175	62.9	11	62.3	13	
523	62.5	12	63.4	9	
138	61.9	13	60.0	21	
532	61.8	14	63.3	10	
SVI	61.7	15	62.5	11	2

[a] Number of family differences within ranks 1-5, 1-10, and 1-15.

Table 6. Comparison of adjusted and unadjusted score of tipmoth damage for nonfertilized plots of loblolly families

Family	RCB unadjusted score	Rank	Lattice adjusted score	Rank	Number of changes [a]
517	6.2	1	4.6	20	
197	6.0	2	5.1	9	
55	6.0	3	5.1	11	
557	6.0	4	5.3	7	
447	5.8	5	5.6	3	4
522	5.8	6	6.7	1	
596	5.8	7	5.4	4	
456	5.5	8	4.3	25	
526	5.5	9	4.9	14	
SVI	5.2	10	4.6	22	5
453	5.2	11	4.7	18	
455	5.2	12	5.0	12	
182	5.2	13	4.4	23	
137	5.0	14	5.0	13	
181	5.0	15	3.8	31	6

[a] Number of family differences within ranks 1-5, 1-10, and 1-15.

CONCLUSIONS

Since a primary function of progeny testing is the evaluation of genotypes by the determination of family means, any increase in the accuracy of determination is important. The lattice design and analysis did a satisfactory job of accounting for environmental variation and gave an increase in precision. Although family significance was not greatly changed, the lattice provided adjusted means which could be used with confidence to evaluate families. An analysis using the adjusted means and a RCB model gave large increases in significance, but statistical considerations for this procedure need to be determined. Lattice designs may be helpful in certain situations and should be given due consideration when applicable.

LITERATURE CITED

Bridgwater, F.E., J.T. Talbert, and D.L. Rockwood. 1983. Field design for genetic tests of forest trees. Pages 28-38 in Progeny Testing of forest trees. Proc. Workshop Progeny Testing. June 15-16, 1982, Auburn, AL. 68 pp.

Cochran, W.G., and G.M. Cox. 1957. Experimental design. 2nd ed. Wiley, New York.

Duba, S.E., R.M. Patterson, and J.F. Goggans. 1982. Intensive culture deserves intensive analysis: The use of a lattice square design to evaluate family and fertilizer effects. Proc. Seventh N. Am. For. Biol. Workshop: 105-112.

Lester, D.T. and G.R. Barr. 1965. Provenance and progeny tests in red pine. For. Sci. 11:327-340.

McKinley, C.R. 1983. Objectives of progeny tests. Pages 2-5 in Progeny testing of forest trees. Proc. Workshop Progeny Testing. June 15-16, 1982, Auburn, AL. 68 pp.

Synder, E.B. 1966. Lattice and compact family block designs in forest genetics. Joint Proc. second genet. Workshop SAF and Seventh Lake States For. Tree Improv. Conf. US For. Serv. Res. Pap. NC-6:12-17.

Wright, J.W. 1978. An analysis method to improve statistical efficiency of a randomized complete block design. Silvae genet. 27:12-14.

ALTERNATIVE DESIGNS FOR PROGENY TESTING SLASH PINE

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Abstract.--Juvenile performance of slash pine progenies in row, block, and Nelder's plots was compared. Progeny x planting density and progeny x competition level interactions were minimal in individual tests. Correlations of progeny performance across tests were positive but generally non-significant. The feasibility of close spacing, short-term assessments of progenies is uncertain.

Additional keywords: *Pinus elliottii* var. *elliottii*, genetic tests, early evaluation, spacing.

Progeny tests of slash pine (*Pinus elliottii* var. *elliottii* Engelm.) have traditionally involved row plots and operational spacings. Under such conditions, reliable evaluation of slash pine parents has required 10 or more years. Progress in advanced generations is constrained by the time required to make field evaluations and selections, and numerous alternatives to long-term field testing are being explored (e.g., Waxler and van Buijtenen, 1981; Franklin, 1979; Lambeth et al., 1982). Recent field tests have provided data to critique some design alternatives for progeny evaluation.

METHODS

In 1978 and 1979, St. Regis Paper Company established 23 progenies in six tests near Cantonment, Florida (Table 1). Two 1978 plantings used nine progenies in 1) a split plot design involving two competition levels (pure = all trees of the same progeny, and maximum = each measurement tree surrounded by eight trees of the other eight progenies) in block plots at two densities (Test 8-78-1), and in 2) Nelder's plots (progenies assigned to spokes) representing 8 densities (Test 8-78-2). The 1979 plantings included as many as 23 progenies in pure vs. maximum competition block plots (Tests 8-79-3 and 8-79-4), Nelder's plots (Test 8-79-5), and 10-tree row plots (Test 8-79-6). Five- and four-year total height, DBH, rust incidence, and survival, respec-

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Table 1. Description of slash pine progeny tests included the analyses.

Test	Location in Florida/ Planting Year	Design
8-78-1	Cantonment/1978	RCB[1], 2 reps; main plots, 1121 and 2242 trees/ha; subplots, 9 progenies; sub-sub-plots, pure and maximum competition
8-78-2	Cantonment/1978	RCB, 6 reps; 9 progenies; 8 densities from 472 to 3089 trees/ha
8-79-3	Cantonment/1979	RCB, 4 reps; 9 progenies in main plots; sub-plots, pure and maximum competition, row plots
8-79-4	Cantonment/1979	RCB, 4 reps; 9 progenies in main plots; sub-plots, pure and maximum competition
8-79-5	Cantonment/1979	RCB, 6 reps; 23 progenies; 8 densities from 472 to 3089 trees/ha
8-79-6	Cantonment/1979	RCB, 6 reps; 18 progenies in 10-tree row plots
0-58	Cantonment/1977	RCB, 3 reps; main plots, 1223 and 2446 trees/ha; subplots, 24 progenies plus check lot
0-59	Perry/1977	RCB, 3 reps; main plots, 1223 and 2446 trees/ha; sub-plots, 22 progenies plus check lot in block plots
0-60	Yulee/1977	RCB, 3 reps; main plots, 1223 and 2446 trees/ha; sub-plots, 22 progenies plus check lot in block plots
10-N	Gainesville/1980	RCB, 9 reps; 33 progenies in 7-tree spokes; 5 densities from 4300 to 43100 trees/ha
11-P	Trenton/1980	RCB, 3 reps; 14 progenies in 25-tree block plots
11-N	Trenton/1980	RCB, 8 reps; 23 progenies in 7-tree spokes; 5 densities from 4300 to 43100 trees/ha
11-S	Trenton/1980	CRD[2], 3 reps; 3 progenies in 25-tree block blocks; 3 densities, 6667, 10000, and 20000 trees/ha

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[1] Randomized complete block design.
[2] Completely randomized design.

tively, are reported for these studies.

Three 'wide' progeny tests established in 1977 on lands of ITT-Rayonier, Buckeye Cellulose Corporation, and St. Regis consisted of up to 24 progenies, with 13 progenies and a standard check lot common to all three tests, assigned to pure block plots at two densities. The 1980 plantings on properties of the University of Florida and ITT-Rayonier had block and Nelder plot components. In Test 11-P, progenies were planted in 25-tree block plots at 10,000 trees/ha. Three progenies were used in 25-tree block plots at three densities in Test 11-S. Nelders plots allocated as many as 33 progenies to spokes at five densities in Tests 10-N and 11-N.

Analyses of variance were performed for each study using appropriate models. Main effects and associated interactions were assessed at the 5% significance level. Clonal evaluations used for comparison with ratings derived from the above tests were based on individual tree volumes in numerous row-plot progeny tests planted at operational densities. Standardized evaluations relative to a check lot in each 5- to 10-year-old test were combined across tests to develop composite evaluations. Consistency of progeny performance across the various tests was based on correlation of progeny means (or clonal evaluations) in pairs of tests.

RESULTS AND DISCUSSION

The early growth observed in the various tests ranged from average to good (Table 2). Tests at Cantonment were located on good sites that had been used for agriculture prior to test establishment; tree size in Test 0-58, for example, was much greater than typically achieved on the flatwoods sites represented by Tests 0-59, 0-60, and 10-N. Test 11 was also situated on an above average site.

Competition among trees at the planting densities included in Tests 8-78-1, 8-79-3, 8-79-4, 8-79-6, 0-58, 0-59, and 0-60, was much less intensive than that created by the high planting densities of Tests 8-78-2, 8-79-5, 10-N, 11-P, 11-N, and 11-S at these young ages. The higher densities in Tests 8-78-1 and 0-58 were just beginning to have significant effects on tree DBH and/or plot volume at age 5. The extremely high densities in Tests 10-N, 11-N, and 11-S influenced tree height and/or DBH by age 3.

Progeny variation was observed in many tests but was somewhat determined by prior selection of progenies for the tests. The nine progenies in Tests 8-78-1 and 8-78-2 were a randomly chosen group of relatively untested clones, and their range in growth potential was evident as significant differentials in Test 8-78-1. Progenies in the other tests were representative of good performing clones typically growing 8 to 48% better than unimproved trees. Tests, such as 8-79-5, 8-79-6, 0-58, 10-N, and 11-N, including a large number of progenies had significant progeny differences.

Progeny x density and progeny x competition interactions, in terms of individual tree size, were remarkably minimal within tests (Table 3), despite varying progeny groups and competition levels. For example, in Test 8-78-1, progenies which grew best at 1121 trees/ha also tended to grow best at 2242 trees/ha. Only DBH of the 23 progenies in Test 8-79-5 was non-uniformly

Table 2.--Summary of growth in the slash pine tests analyzed.

Test	Age (yrs)	Height (m)	DBH (cm)	Rust (%)	Survival (%)
8-78-1	5	4.15	5.97	33.3	86.7
8-78-2	5	3.90	5.66	20.9	92.7
8-79-3	4	3.55	4.78	-	-
8-79-4	4	3.62	5.00	28.6	93.6
8-79-5	4	3.34	4.67	25.6	94.5
8-79-6	4	3.71	5.33	26.6	88.7
0-58	5	4.55	7.15	-	88.4
0-59	5	3.31	4.97	-	92.6
0-60	5	3.37	4.95	-	86.9
10-N	3	1.80	1.71	-	-
11-P	3	2.83	3.31	-	96.7
11-N	3	2.67	2.85	-	-
11-S	3	2.93	3.69	-	98.9

affected by eight planting densities. Otherwise, progenies responded similarly to 1) intergenotypic mixes of pure (half-sib neighbors) and maximum interprogeny competition such as would be found in non-contiguous plots, and 2) planting densities that bracket the usual range for pulpwood plantations (Tests 8-78-1, 0-58, 0-59, and 0-60), extend typical commercial densities (Test 8-78-2), or utilize very close spacings (Tests 10-N, 11-N, and 11-S).

Across tests that shared the same progenies but had different designs, progeny performance was statistically consistent in only one case (Table 4). Eighteen progenies in the 10-tree row plots of Test 8-79-6 (planting density of 1345 trees/ha) performed similarly in the 8-tree row plots (encompassing planting densities from 472 to 3089 trees/ha) of Test 8-79-5. Progeny stability over competition level and planting density (8-78-1 vs. 8-78-2, 8-79-3 vs. 8-79-5, 8-79-4 vs. 8-79-5), block plots and row plots (8-79-3 vs. 8-79-6, 8-79-4 vs. 8-79-6), and block plots and planting density (11-P vs. 11-N, 11-P vs. 11-S, 11-N vs. 11-S) was not indicated statistically, perhaps due to the uniformity and limited number of progenies involved.

Progeny performance in only one of the 13 tests examined was related significantly to clonal evaluations based on routine progeny tests (Table 5), as nineteen progenies in the block plots of Test 0-58 were similar to their row-plot evaluations. The inconsistency of the correlations in the other tests may reflect the variation frequently observed in progeny performance in single tests. For example, 10 of the 13 progenies common to Tests 0-58, 0-59, and 0-60, surpassed the standard check lot in at least two of the tests (Goddard et al., 1982), in accordance with their row-plot evaluations. The use of height as the progeny characteristic in most of these tests may also have contributed to low correlations with clonal volumes, although the volumes of progenies in Tests 0-59 and 0-60 were poorly related to clonal

Table 3.--Significance of progeny x density and progeny x competition interactions within 13 tests.

Test	Factor	Height	DBH
8-78-1	1121 vs. 2242 trees/ha	NS	NS
	Pure vs. Maximum Competition	NS	NS
8-78-2	8 Densities from 472 to 3089 trees/ha	NS	NS
8-79-3	Pure vs. Maximum Competition	NS	NS
8-79-4	Pure vs. Maximum Competition	NS	NS
8-79-5	8 Densities from 472 to 3089 trees/ha	NS	*
8-79-6	None	-	-
0-58	1223 vs. 2446 trees/ha	NS	NS
0-59	1223 vs. 2446 trees/ha	NS	NS
0-60	1223 vs. 2446 tres/ha	NS	NS
10-N	5 Densities from 4300 to 43100 trees/ha	NS	NS
11-P	None	-	-
11-N	5 Densities from 4300 to 43100 trees/ha	NS	NS
11-S	6667, 10000, and 20000 trees/ha	NS	NS

NS and * = Nonsignificant and significant at the 5% level, respectively.

Table 4.--Correlations (r) of slash pine progeny means for height across tests having different design factors but sharing common progenies.

Test Comparisons	No. of Progenies	r	Range of Progeny Means 1st Test	Range of Progeny Means 2nd Test
			----------(m)	---------
8-78-1 vs. 8-78-2	9	.402	3.98-4.52	3.46-4.08
8-79-3 vs. 8-79-5	9	.614	3.18-3.83	3.02-3.71
8-79-3 vs. 8-79-6	9	.597	3.18-3.83	3.30-3.90
8-79-4 vs. 8-79-5	9	.456	3.40-3.80	2.96-3.65
8-79-4 vs. 8-79-6	9	.424	3.40-3.80	3.30-4.11
8-79-5 vs. 8-79-6	18	.648*	2.96-3.71	3.30-4.11
11-P vs. 11-N	13	.378	2.65-2.99	2.53-2.95
11-P vs. 11-S	3	.995	2.78-2.97	2.35-3.02
11-N vs. 11-S	3	.669	2.75-2.91	2.35-3.02

*= Significant at the 5% level.

Table 5.--Correlations (r) of slash pine progeny means for height in various progeny tests with composite clonal evaluations.

Test	No. of Progenies	r	Test	No. of Progenies	r
8-78-1	8	.397	0-58[1]	19	.486*
8-78-2	8	.369	0-59[1]	19	-.120
			0-60[1]	17	.132
8-79-3	9	-.204			
8-79-4	9	-.359	10-N	32	-.016
8-79-5	23	-.249	11-N	24	.224
8-79-6	18	-.142	11-P	17	.055
			11-S	3	.914

[1] Progeny means were for individual tree volume
* = Significant at the 5% level.

evaluations. Another explanation may be the relatively young ages (i.e., small tree sizes) of many of the tests involving somewhat conventional planting densities. Juvenility may not be a sufficient explanation, however, for the correlations observed for the high density plantings, namely Tests 10-N, 11-N, and 11-P.

CONCLUSIONS

Results to date suggest that slash pine progenies, especially those selected by traditional progeny tests, have low degrees of progeny x competition level and progeny x planting density interactions within a designed test, unlike the observation of Stoneypher and McCullough (1981) of family x density interaction in Douglas fir. Consistency of progeny performance across different testing regimes (block plots, row plots, and competition levels) in different tests has not been sufficiently demonstrated. Juvenile growth of the progenies observed in these tests does not correspond closely enough with conventional clonal evaluations to advocate these alternative procedures. Closely-spaced, short-rotation evaluation systems, as observed by Franklin and Squillace (1973) and advocated by Franklin (1979), require further study.

LITERATURE CITED

Franklin, E. C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genetica 28(5-6):207-212.

Franklin, E. C., and Squillace, A. E. 1973. Short-term progeny tests and second generation breeding in slash pine. Can. J. For. Res. 3:165-169.

Goddard, R. E., Rockwood, D. L., and Kok, H. 1982. Cooperative Forest Genetics Research Program 24th Prog. Rept., Univ. Fla. Sch. For. Res. and Conserv. Res. Rept. No. 33. 25 pp.

Lambeth, C. C., Stonecypher, R. W., and Zobel, B. J. 1982. Early testing of Douglas-fir in phytotron environments - the effect of selection trait and genotype-environment interaction. Proc. 7th. N. Amer. For. Biol. Wkshp.:137-148.

Stonecypher, R., and McCullough, R. 1981. Evaluation of full-sib families of Douglas-fir in a Nelder design. Proc. 16th S. For. Tree Imp. Conf.:55-76.

Waxler, M. S., and van Buijtenen, J. P. 1981. Early genetic evaluation of loblolly pine. Can. J. For. Res. 11:351-355.

GROWTH OF TISSUE CULTURE PLANTLETS OF LOBLOLLY PINE IN A NURSERY AND GREENHOUSE[1/]

L. A. Wisniewski, S. E. McKeand and R. E. Brooks[2/]

Abstract.--Tissue culture plantlets of loblolly pine (*Pinus taeda* L.) were grown in a nursery and a greenhouse in the summer of 1982 to compare the growth and developmental patterns of the trees in the two environments. The plantlets were compared to seedlings, excised embryos (embryos removed from the female gametophyte and grown in tissue culture medium), and rooted hypocotyls (embryos cut at the mid hypocotyl region and rooted "in vitro").

The initial growth rate of all four plant types was slower in the nursery than in the greenhouse. By the fourth month, nursery performance equalled or exceeded greenhouse performance with regards to height growth in all four plant types. However, the plantlets and excised embryos grew significantly slower in the greenhouse. The reduction in growth of the plantlets and excised embryos in the greenhouse may result from restriction of root growth in containers.

INTRODUCTION

The use of tissue culture as a tool in reforestation programs has become very promising in recent years. With the improvement of laboratory and greenhouse techniques, it is now possible for plantlets to be produced from several important forest tree species (Mott 1981). Among these species, loblolly pine (*Pinus taeda* L.) has been studied extensively by researchers at North Carolina State University. Over 4000 plantlets from 30 different familes have been produced and established in various greenhouse, nursery and field experiments.

Growth of loblolly pine plantlets in the greenhouse has been reported in a few experiments (Leach 1979, Amerson *et al*. 1981, McKeand and Wisniewski 1982, McKeand 1983). The growth patterns of the plantlets appear to be different than seedlings grown under similar conditions. Plantlets have a slower growth rate initially when compared to seedlings (McKeand and Wisniewski 1982, McKeand 1983). This lag period arises while the plantlets are becoming acclimated to the greenhouse environment. Once the plantlets become acclimated, the relative growth rates between the plantlets and the seedlings are about equal (McKeand 1983).

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Although there have been reports of plantlet growth in the greenhouse, there have been no reports of growth in an outdoor nursery. The ability for plantlets to survive and grow in a pine seedling nursery would allow for the operational production of plantlets in a nursery in future years.

This experiment was initiated to study the survival and growth of the loblolly pine tissue culture plantlets in a nursery bed and to compare growth between the nursery and the greenhouse environments.

MATERIAL AND METHODS

A range of plant types were produced to form a gradient from a tissue culture plantlet composed of both an adventitious shoot and root to a normal seedling with epicotyl, hypocotyl, cotyledons and radicle. The tissue culture plantlets and intermediate plant types (i.e. rooted hypocotyls and excised embryos) were produced in the laboratory from a mix of five open-pollinated families as follows:

Tissue Culture Plantlet -Multiple shoot were initiated on an excised cotyledon. After the shoot elongated, it was the rooted on agar medium. Both the shoot and the root were adventitious (Mott and Amerson 1981).

Rooted Hypocotyl -Seeds were germinated in 1% H_2O_2 and when the radicle emerged about 5 mm, the embryo was removed. Embryos were grown on a sterile agar nutrient medium until the epicotyl started to elongate. The embryo was then cut at mid-hypocotyl (about 5 mm below the cotyledons) and placed on root initiation medium. Only the roots were adventitious.

Excised embryo -The same procedure was followed as for the rooted hypocotyls except the radicle was not removed. This procedure produced a "normal" seedling grown in tissue culture medium.

All plant types were transplanted to the soil once the shoot was 1-2 cm long and the roots were approxiamtely 5 mm long (Figure 1). Seeds were sown 1 to 3 weeks after the plantlets were transferred from the lab. Seeds germinated and grew in 164 ml (10 cu. in.) RL Super Cells® in a greenhouse. The plantlets, rooted hypocotyls, and excised embryo were grown along with the seedlings using methods of Amerson et al. (1981). During the first 4 weeks in the greenhouse mist bench, a solution of Peters® 15-30-15 at 30 ppm N was applied 3-5 days per week to wet the upper soil surface. When the trees were removed from the mist and placed on a standard greenhouse bench, Peters® 20-19-18 at 39 ppm N was applied 3-6 days per week. The fertilizer solution was added until it dripped from the container. The trees were watered heavily once a week to prevent excessive fertilizer salts accumulation.

After approximately six weeks in the greenhouse, half of the trees were transplanted to Federal Paper Board's nursery in Lumberton, North Carolina. They were planted bare root using a dibble at a 7.6 cm x 15.2 cm (3" x 6") spacing. Root length and dry weight and shoot length and dry weight were measured in a 20 tree subsample of each type at the time of transplant to the nursery.

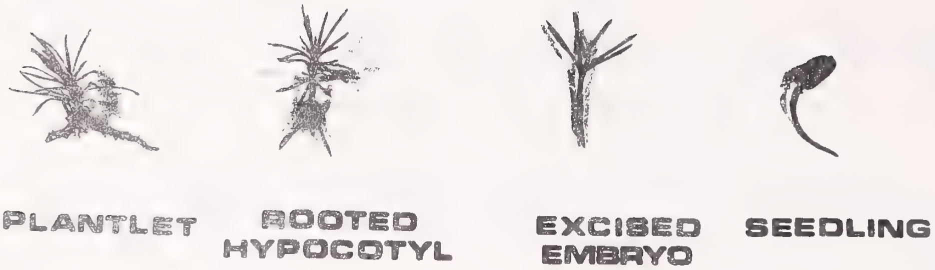

Figure 1.--Loblolly pine tissue culture plantlet, rooted hypocotyl and excised embryo when transplanted to greenhouse compared to newly germinated seed.

Conventional nursery practices were used to grow the trees through the nursery growing season. Five hundred-sixty kilograms per hectare of 5-10-30 fertilizer were applied in February. Ammonium nitrate (112 kg/ha) was applied five times through the growing season. One application of 20-20-20 (11.2 kg/ha) in early August and one application of muriate of potash (78.5 kg/ha) in late August was also added. Trees were irrigated as necessary to provide one inch of water per week. Weeds were controlled by hand.

The remaining trees were left in their original containers in the greenhouse on the North Carolina State University campus in Raleigh, N. C.. The trees were watered every day and fertilized with Peters® 20-19-18 at 39 ppm N three days per week. They were watered and fertilized until the solution dripped from the bottom of the container.

The experimental design was a randomized complete block in two locations (i.e. greenhouse and nursery). Within each location, the four plant types where randomized in four blocks with 7 plants/type/block/location for a total of 224 trees.

Height was measured every thirty days from May to October, 1982 in both the nursery and the greenhouse. Analyses of variance was performed to determine differences between treatments and plant types for shoot growth.

RESULTS AND DISCUSSION

Survival of all four plant types was excellent in both the greenhouse and nursery, with an average of 100 and 96 percent, respectively (Table 1). The rooted hypocotyls had the lowest percent survival (91%) in the nursery because of their very small initial size. The tissue culture plantlets had 97% survival in the nursery.

Table 1.--Characteristics of different plant types used in the study.

	When Transplanted in May			
Plant Type	Stem Height (cm)	Main Root Length (cm)	Root Dry Weight (gr.)	Survival in August
Tissue Culture Plantlets	1.4	8.8	0.013	97%
Rooted Hypocotyls	0.7	6.0	0.003	91%
Excised Embryos	1.6	15.6	0.006	98%
Seedlings	4.5	-	0.014	99%

Early growth in the nursery was slower than in the greenhouse for all plant types (Figure 2). This was expected since there was a lag period while the trees became acclimated to the nursery. In the nursery, plantlets had the highest percent growth for the first 30 days, at 320 percent compared to 140 percent for the seedlings (Table 2). Although percent growth of plantlets in the nursery was slower in the second month, it had surpassed the percent growth in the greenhouse. From this time on the seedlings and the plantlets grew about the same, suggesting that the plantlets would have been the same height as the seedlings if their initial sizes had been equal (Figure 2b).

Growth in the greenhouse followed the same pattern as growth in the nursery (Figure 2a.) The plantlets had a much higher percent growth initially than the seedlings. After the first month, both the plantlets and the seedlings had approximately the same percent growth.

Table 2.--Percent growth in the nursery and greenhouse for the different plant types throughout the growing season.

	0-30 Days		30-60 Days		60-90 Days		90-120 Days		120-150 Days	
	N	G	N	G	N	G	N	G	N	G
Seedlings	140	413	126	56	63	9	32	7	5	3
Plantlets	320	934	78	11	93	6	42	16	5	7
Excised Embryos	166	794	144	43	99	10	43	7	10	8
Rooted Hypoctyls	267	1374	143	86	104	9	61	13	13	8

N = nursery
G = greenhouse

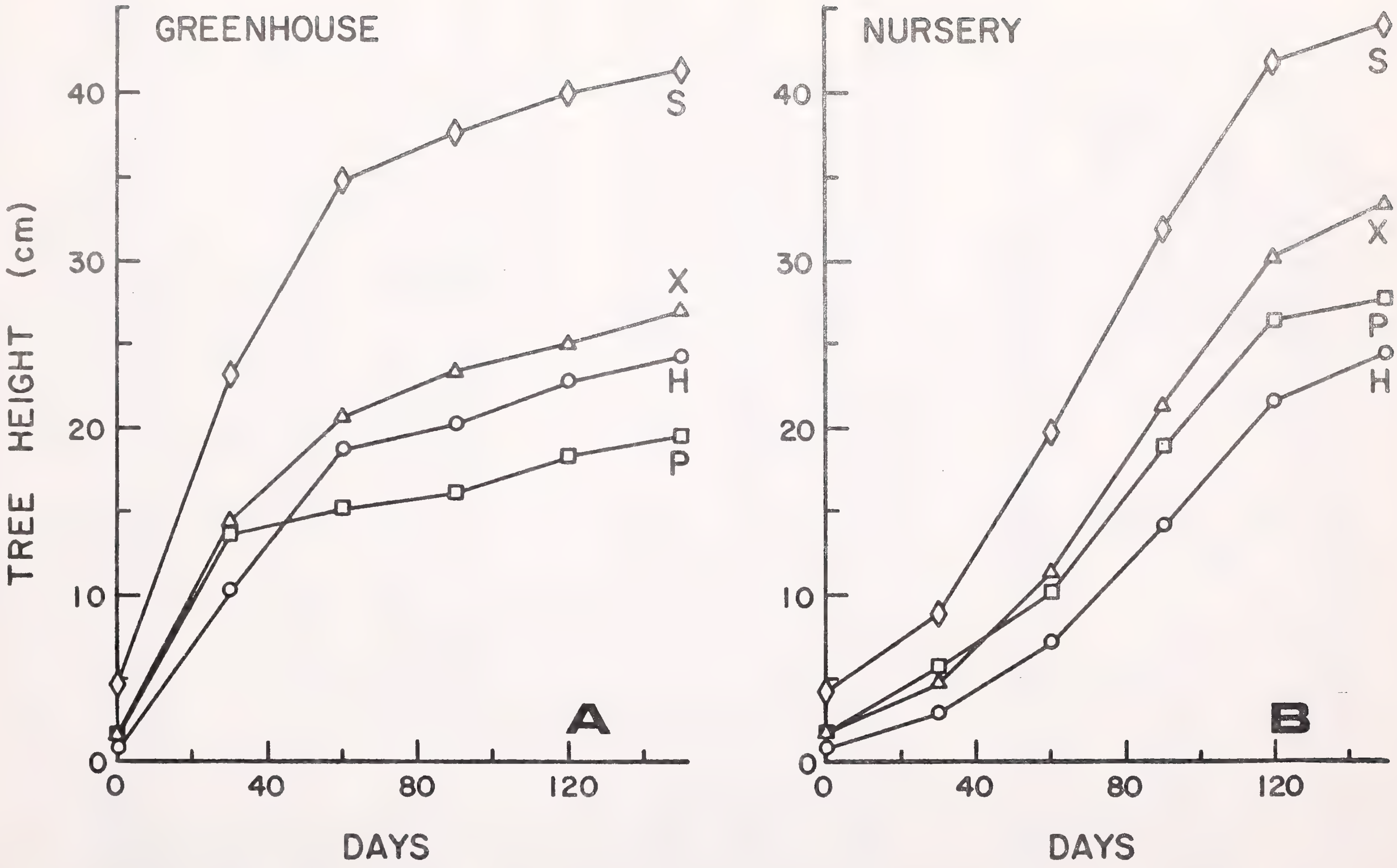

Figure 2.--Height growth of loblolly pine tissue culture plantlets, rooted hypocotyls, excised embryos and seedlings in the (A) greenhouse and (B) nursery.

Although the initial growth rate was slower in the nursery, subsequent growth equalled and, with some plant types, surpassed the growth in the greenhouse (Figure 3). By the fourth month (120 days), there was no significant difference in performance between the nursery or greenhouse in either the seedlings or rooted hypocotyls with regards to height growth. However, the height of the plantlets and excised embryos, in the nursery, had surpassed those in the greenhouse at three and four months, respectively, causing the interaction between the locations and plant types to change with time (Table 3). The largest interaction occurred while the trees where becoming acclimated during the first month of growth at day 30. Once the height in the nursery reached that in the greenhouse at 150 days, the interaction was much less significant.

The location by plant type interaction was caused primarily by the poorer growth of the plantlets and excised embryos in the greenhouse as demonstrated by the crossover of their growth curves (Figure 3a and 3c). The reduction in height growth of the plantlets and excised embryos in the greenhouse apparently occurred when the root growth was restricted by the containers. This reduction was not seen in the seedlings because of their superior root morphology (McKeand and Wisniewski 1982). Plantlets typically have few lateral roots and a reduced root surface area for nutrient uptake (McKeand 1983). The restriction of the short, large diameter, non-fibrous root system in the containers probably limited root growth and ultimately reduced height growth of the plantlets. The reduced height of excised embryos can also be explained by the root growth constriction of the containers. When the embryos are exposed to the H_2O_2, during culturing, the radicle is sometimes killed thus producing an adventitious root system. When an adventitious root system is produced, the excised embryos exhibit a reduced height growth similar to the plantlets (McKeand and Wisniewski unpublished). The restriction of root growth is expected with the rooted hypocotyls since they also possess an adventitious root system. However, their small initial size probably allowed for the continued good growth since their root system had not reached a size that would be constrained by the container. Had the rooted hypocotyls been grown in the containers for a longer period of time, we would expect to see a similar reduction in growth.

Table 3.--Analysis of variance for stem height.

	Probability of a greater F for height measurements						
		Days					
Source	d.f.	0	30	60	90	120	150
Corrected Total	223						
Location	1	.89	.01	.001	.06	.03	.001
Plant type	3	.001	.01	.001	.01	.001	.001
Location x Type	3	.22	.01	.001	.01	.02	.08
Rep/Location	6	.07	.10	.001	.03	.02	.08
Type x Rep/Location	18	.79	.38	.03	.14	.07	.05
Error	192						

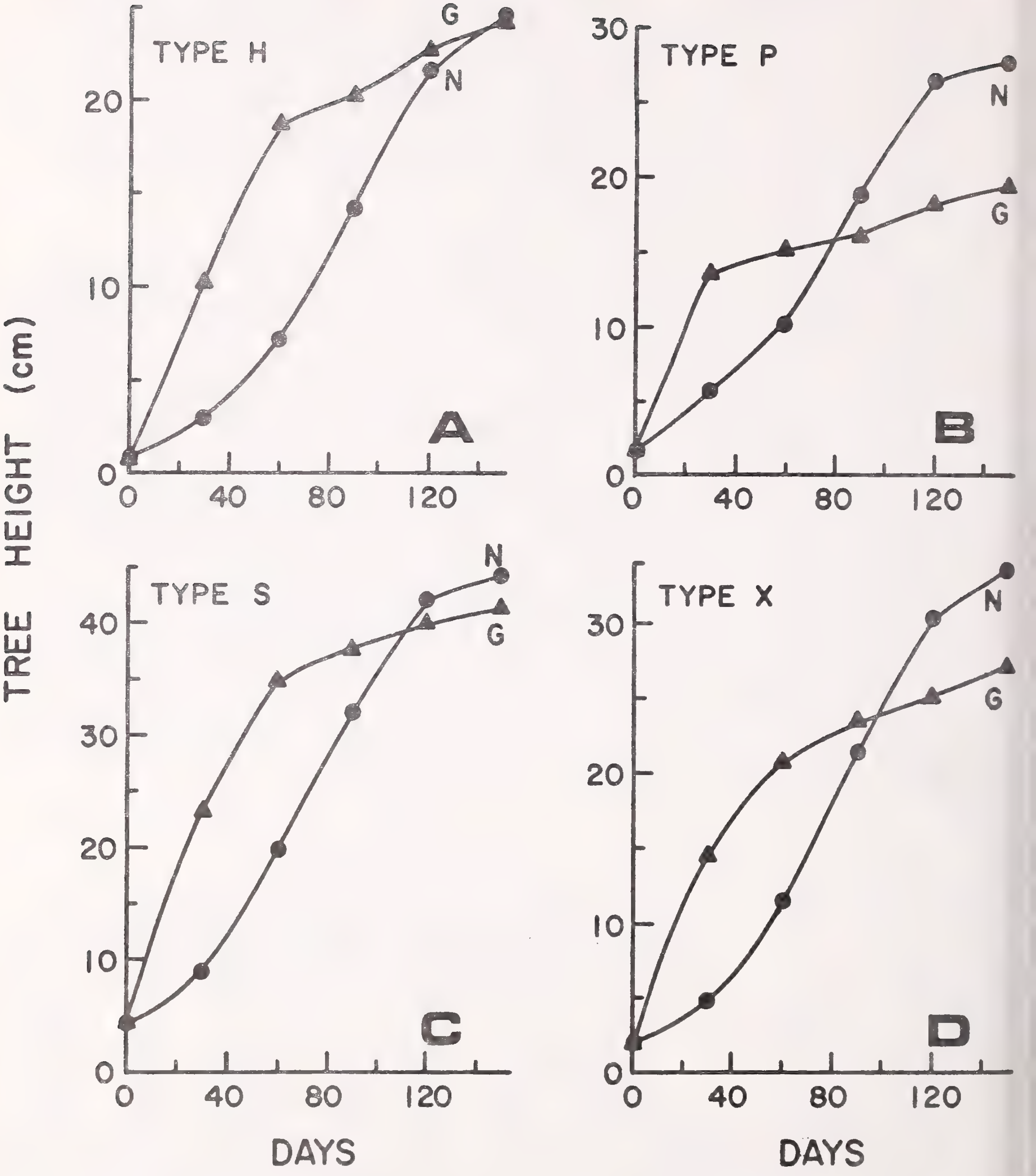

Figure 3.--Height growth in the nursery and greenhouse of loblolly pine (A) rooted hypocotyls, (B) tissue culture plantlets, (C) seedlings and (D) excised embryos.

CONCLUSIONS

The excellent survival and good growth of the tissue culture plantlets in the nursery showed that conventional seedling nursery practices can be used to grow plantlets to a size suitable for field planting. Future propagation systems for plantlets may need to utilize nurseries to make tissue culture economically feasible.

The growth reduction of the plantlets in the greenhouse suggests the need for further study of the root systems of the plantlets. The trees used in this study are being destructively sampled to measure several root and shoot characteristics. The results will be reported in a later paper.

ACKNOWLEDGMENTS

The use of trade name does not imply endorsement of products named nor criticism of products not named.

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LITERATURE CITED

Amerson, H. V., McKeand, S. E. and Mott, R. L. 1981. Tissue culture and greenhouse practices for the production of loblolly pine plantlets. Proc. 16th South. For. Tree Impr. Conf. p. 168-173.

Leach, G. N. 1979. Growth in soil of plantlets produced by tissue culture. Tappi 62(4):59-61.

McKeand, S. E. 1983. Growth and development of tissue culture plantlets of loblolly pine in a greenhouse. Ph.D. Thesis, North Carolina State Univ., Raleigh. 65 p.

McKeand, S. E. 1981. Loblolly Pine Tissue Culture: Present and Future Uses in Southern Forestry. School of For. Resources, Tech. Rept. No. 64, N. C. State Univ., 50 p.

McKeand, S. E. and Wisniewski, L. A. 1982. Root morphology of loblolly pine tissue culture plantlets. Proc. 7th North Amer. For. Biol. Workshop, p. 214-219.

Mott, R. L. and Amerson, H. V. 1981. A tissue culture process for the clonal production of loblolly pine plantlets. N. C. Ag. Res. Service., Tech. Bul. No. 271, 14 p.

Mott, R. L. 1981. Trees. In: Principles and practices of cloning agricultural plants via _in vitro_ techniques (B. V. Conger, ed.) CRC Press, Boco Raton, FL.

PERFORMANCE OF SINGLE FAMILY VERSUS MIXED FAMILY PLANTATION BLOCKS OF LOBLOLLY PINE

C. G. Williams[1], F. E. Bridgwater[2], and C. C. Lambeth[3]

Abstract.--Sixteen loblolly pine (*Pinus taeda* L.) families were planted in single family and in mixed family (noncontiguous) plots in 1978. The original purpose of the study was to compare growth and straightness between the two stand types. Preliminary results from measurements at age four indicated that single family plots performed better than mixtures of the same families. Family by stand type interactions were not estimable for growth traits and were small for quality and disease resistance. Family performance correlated well with progeny test assessments.

Additional keywords: Intergenotypic competition effects, single family plantation blocks, *Pinus taeda*.

INTRODUCTION

Intergenotypic competitive effects can be manifested as a yield increase for all genetic entries in one stand composition type over another. For example, mean grain yield from pure plots was greater than the mean of mixtures of tropical rice varieties (Jennings and Aquino, 1968). By contrast, mean yields did not differ by stand types for soybeans (Sumarno and Fehr, 1980; Hinson and Hanson, 1962).

Cereal yields in monoculture are inversely related to the competitive ability of the genotype (Hamblin and Donald, 1974; Donald and Hamblin, 1976). Rice varieties have shown this most consistently. The taller, leafier plant types tended to compete effectively but had low grain yields (Jennings and deJesus 1968). Strong competitive ability of this type has been a deterrent to advances in plant breeding programs because it distorts genetic variances and, consequently, selection (Hamblin and Rosielle, 1978).

Yield differences have been observed with loblolly pine families as well. Five Piedmont loblolly pine families were planted in single family and mixed family plots to increase the size and number of plantable seedlings. Single family plots had taller seedlings than the mixed plots after the first year (Dierauf, Virginia Division of Forestry, unpublished data). The germination rates among families accounted for the higher yields rather than inherent growth differences among families (N.C. State Cooperative Annual Report 1975).

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Several intergenotypic competition studies have been conducted with forest tree seedlings (Adams et al. 1973; Tauer, 1975; Adams 1980) but the results have shown no consistent relationship between yield and intergenotypic competition. Results from two recently measured field studies should address this question (Sam Land, Mississippi State University, pers. comm.; Lambeth, unpublished data).

The following study was used to answer two questions:

1) Do yields from single family plantations approximate yields from a mixture of families?

2) How do families in pure blocks compare with the commercial check for straightness, rust resistance and growth?

METHODS

Procedure and Test Design

The seeds were stratified and sown in containers then later arranged in the field design to maintain the same competitive relationships from greenhouse to outplanting. The seedlings were outplanted at 3 m spacing in southeastern N.C. on a poorly drained sandy site. Seedlings received tip moth control the first year and weed control the second year.

Height (meters), diameter at breast height (centimeters), rust resistance and straightness[4/] were tallied after four growing seasons in the field. Volume (cubic decimeters) was estimated from height * dbh^2. Mortality was low (2%) and the lowermost branches had not begun to prune off although crown closure had begun. Sixty-eight percent (4901 trees) of all test trees, including borders, had some sign of fusiform rust [Cronartium quercum (Berk.) Miyabe ex Shirai f. sp. fusiforme].

Sixteen half-sib families that represented a wide range with respect to growth, straightness, and rust resistance (as evaluated from genetic tests) were selected. A commercial check collected from seed production areas in eastern North Carolina was also included; this is the same check used in Weyerhaeuser Company's first-generation High Wood Density progeny tests.

A sets-in-blocks design with three blocks was used. In each block, six seedlots were grouped in each of four sets. Four different single family plots (64 trees per plot) were assigned to a set within each block and were confounded with sets. The commercial check and a bulked mix of all sixteen families were included in each set.

Statistical Analyses

The data analyses were performed with the assistance of the Statistical Analysis System package (SAS Institute 1979). Set and block * set interaction

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[4/] N.C. State Industry Pine Cooperative straightness score 1-6.

terms were not significant at the 95% confidence level so the data was pooled over sets. Blocks and family terms were random. Stand composition type was a fixed term. The analyses were done on a plot mean basis.

The eight-year progeny test performance ranks were based on unitless measures that represented the number of standard deviations above or below the mean of all families tested in the High Wood Density breeding program. This measure was used because of the family imbalance across tests and across two overlapping breeding regions that have now been combined.

Rust resistance was measured as the number of trees without stem galls in both the family yield trial and the progeny test data. An arcsin$\sqrt{\overline{Y}}$ transformation was used to approximate a normal distribution.

RESULTS AND DISCUSSION

Single Family Plots Versus a Mixture of Families

Due to the young age of the test and the fact that competition influences were not strong, no firm conclusions can be drawn regarding yield in pure blocks versus mixtures of families. However, the single family plots have a slight growth advantage over mixed plots which is statistically different at the 95% level (Table 1). The mean of single tree plots is 3.1% (.12 meters) greater than that for the mixed family plots; the volume increment was 9.0% (1.4 dm^3).

Table 1.--Fourth-year results from the family yield: the values from the F-test of significance for family, stand type (mixed versus pure stand) and family-by stand interaction terms for height, volume straightness and rust resistance.

Source	df	Height (m) F-value	Volume (dm^3) F-value	Straightness Score F-value	Rust Resistance (% gall-free) F-value
Family	15	2.97*	2.64*	5.00**	4.64**
Stand Type	1	4.76*	5.75*	1.60	2.00
Family * Stand	15	1.89	1.60	1.13	1.67

* $\geq$ 5%
** $\geq$ 1%
*** $\geq$ .1%

This growth advantage is an early indication of a consistent, positive relationship between growth and intrafamily competition. The phenomenon is previously unreported for forest trees.

Rust infection was as severe in the mixture (50% of the trees were rust-resistant) as it was in the single family plots (48%). It is unlikely that the stand types would differ in this respect. The fusiform rust fungus requires alternate hosts, pine and oak (Quercus) thus it did not spread from pine to pine once the stand became infected. Increased rust infection is not likely the consequence of a family block plantation system. Also, straightness was not affected by whether the families were grown in bulked plots or single plots (Table 1).

Family by stand type interaction was not significant at the 95% confidence level for all traits (Table 1). The lack of significance suggested a closer look at the relative efficiency of composite versus pure block plots to estimate the family means for growth traits. This was done to determine if the test was adequately designed to detect biologically important rank changes since this was not one of the objectives at the time of test establishment. Each stand type was then analyzed separately.

The single family (square block) plot design was inadequate to estimate family height means precisely and accurately at this early stage of stand development (Table 2).

Table 2.--A comparison of the relative efficiency of the single family (block plot) design and the mixed family (noncontiguous) design for height within the family yield trial, at age four.

	Single family plot	Mixed family plot
Pr > F-value for family term	.0920	.0005
Block * Family (error) Variance Component	.04	.02
Coefficient of variation	5.6%	3.5%

The block * family (error) term was higher, the family term was non-significant at the $\geq$ 95% level and the coefficient of variation is higher when compared with the mixed family (noncontiguous) plot design which is highly efficient and requires fewer trees per family and fewer replications (Lambeth et al., in press).

The two plot designs represented the extremes for genetic test designs with multiple tree family plots. When replicated three times as in the yield trial the square block plots tend to encompass high levels of within-plot (environmental) error which is reflected in growth. After crown closure growth becomes more uniform and within-plot error tends to diminish. The coefficient of variation among plots generally drop as site capture progresses. Thus, large block plots do not provide accurate and precise estimates of family means by age four when planted at operational spacing unless a prohibitively large number of replications is used (Williams and Lambeth, unpublished data).

Quality traits did not show the same trends as growth traits did. Although neither demonstrated the family * stand interaction term to be statistically important, family differences in straightness and in rust resistance were statistically significant for the separate analyses of both plot designs (Table 3). Bole straightness and rust infection apparently are not as affected by site heterogeneity unaccounted for by the test design as growth traits are.

Table 3.--Analyses of each plot design for rust resistance and straightness - 4-year results of the family yield trial.

	Mixed Family Plot	Single Family Plot
Straightness		
Pr > F Family term	.002	.044
Block * Family Variance (error)	.025	.030
Rust Resistance		
Pr > F Family term	.032	.044
Block * Family Variance (error)	.064	.072

The overall study design was not adequate to assess rank changes from one stand type to another (family * stand interaction) for growth traits. The ability of the two types of plot designs to estimate family means within an allowable margin of error was confounded with any biologically important rank changes.

The differences between plot design were very small for quality traits so the designs were comparable. However, family * stand interaction was not statistically important. Families do not appear to change rank from one stand type to another with respect to straightness and rust resistance.

Realized Genetic Gains

Family ranks correlated well with progeny test ranks (Table 4). The correlations indicated that the rust score had been an effective tool to discern differences among rust-resistant and rust-susceptible genotypes in field tests. It should be noted that the score was effective for loblolly pine progeny tests in North Carolina where rust infection and rust-associated mortality tended to be lower than other parts of the southeastern U.S. The gall/no gall trait may not have been as effective in an area where a large proportion of the trees readily succumbed to the disease. The trait discerned between live trees without rust and trees that survive with rust but does not take in account rust-infected trees that died as a result of the disease (R. J. Weir, N.C. State University, pers. comm.)

Table 4.--Spearman's rank correlation coefficients between 8-year progeny test assessments and 4-year family performance in the yield trial.

Yield Trial	Progeny Test Rust Resistance	 Straightness	 Height	 Volume
Rust Resistance	.621**			
Straightness		.604**		
Height[a/]			.737***	.667**
Volume[a/]				.607**

[a/] These ranks are based on mixed family plot performance only.

***.1% significance level
**1%

Correlations for growth traits reflect the degree to which family ranks from mixed family plots and progeny tests vary together. Since single family plots did not have significant family differences ranks were misleading.

The correlations are high in spite of the fact that family performance for the yield trial was assessed from a single test site at age four and compared with 8-year progeny test data. This attests to the test quality and rapid growth rate of the yield trial.

One other striking consistency emerged from the single family plots. The commercial check (excluded from all other previously reported analyses) was compared with the performance of the sixteen families. Seedlot differences were statistically significant for the single family plot design when the check was included. The check ranked 17 out of 17 for growth and straightness and 11 out of 17 for rust resistance. The differences between the check and the mean of the improved families is 7.3%, 25.3%, 6.9%, and 9.1% for height, volume, straightness and rust resistance respectively (Table 5).

The maternal parent of each of three families included in this test have since been rogued out of the seed orchard so this suggests improvement over the check for planting stock in current use was conservative. These estimates of gain may not reflect what would happen on a range of site types.

Table 5.--A comparison between the commercial check and stand type means.

	Stand Type Means		Commercial Check
	Mixed	Pure	
Height (m)	3.86 ± .15	3.98 ± .21	3.71
Volume (dm^3)	17.86 ± 2.3	19.34 ± 3.1	15.44

SUMMARY AND CONCLUSIONS

Single family plots had a slight overall growth advantage over mixture which indicated a positive relationship between intrafamily competition and growth. However this conclusion is preliminary since competition influences were not strong in this 4-year-old planting. Rust infection was as severe in the family plots as it was in a mixture of the same families. Straightness assessments were also the same in both stand types.

The test was not suited to estimate family * stand interactions so no evidence of rank changes from mixed stands to pure stands could be detected for growth traits. No family * stand interactions were detected for quality traits.

Progeny test ranks (age 8 years) for growth, rust resistance and straightness correlated highly with family performance in the trial. All families showed improvement over the commercial check for growth and straightness.

LITERATURE CITED

Adams, W. T. J. H. Roberds and B. J. Zobel. 1973. Intergenotypic interactions among families of loblolly pine (*Pinus taeda* L.). Theor. Appl. Gen. 43:319-322.

Adams, W. T. 1980. Intergenotypic competition in forest trees. Proc. 6th N. Amer. For. Bio. Wkshop, Edmonton, Alberta.

Donald, C. M. and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agron. 28:361-405.

Hamblin, J. and C. M. Donald. 1974. The relationship between plant form, competitive ability and grain yield in a barley cross. Euphytica (23):535-542.

Hamblin, J. and A. A. Rosielle. 1978. Effect of intergenotypic competition on genetic parameter estimation. Crop Sci. 18(1):51-55.

Hinson, K. and W. D. Hanson. 1962. Competition studies in soybeans. Crop Sci. (2):117-123.

Jennings, P. R. and R. C. Aquino. 1968. Studies on competition in rice. III. The mechanism of competition among phenotypes. Evol. (22):529-543.

Jennings, P. R. and J. deJesus. 1968. Studies on competition in rice. I. Competition in mixtures of varieties. Evol. (22):119-124.

Lambeth, C. C., W. T. Gladstone and R. W. Stonecypher. Statistical efficiency of row and noncontiguous family plots in genetic tests of loblolly pine. Silv. Gen. (in press).

North Carolina State-Industry Cooperative. 1975. Annual Report.

SAS Institute. 1979. SAS User's Guide. Statistical Analysis System Institute, Inc. 494 p.

Sumarno and W. R. Fehr. 1980. Intergenotypic competition between determinate and undeterminate soybean cultivars in blends and alternate rows. Crop Sci. (20):251-254.

Taner, C. G. 1975. Competition between selected cottonwood genotypes. Silv. Gen. 24:44-49.

VARIATION, HERITABILITY AND GAIN IN HARDWOODS

VARIATION AND HERITABILITY OF BRANCHING AND GROWTH CHARACTERISTICS AMONG SYCAMORE PROGENY

Charles J. Jourdain and James R. Olson[1/]

Abstract.--Forty-eight open-pollinated families of American sycamore from 5 seed sources were analyzed at the end of the fifth growing season for variation in height, diameter, live crown, branch angle, and branch frequency. All traits differed significantly among families, while diameter was the only trait which differed among seed sources. All traits were moderately inherited. Mass selection of the best 10 trees without regard to family resulted in genetic gains approximately 3.5 times as great as those from family selection. Direct selection to improve crown form will lead to decreased diameter growth, while selection for diameter will result in trees with larger and more fastigate crowns.

Additional keywords: Platanus occidentalis, live crown, branch angle, branch frequency, open-pollinated families, genetic gain.

American sycamore (Platanus occidentalis L.) plantations are currently being established throughout the southern and central Mississippi River valleys on sites not suitable for eastern cottonwood (Populus deltoides Bartr.). Selection of superior genotypes is needed to maximize the utilization potential of this species. Due to the influence of crown form on growth rate and wood quality (Larson 1962) genetic variation of branching characteristics must be quantified. Variation and inheritance of certain branching traits of sycamore have been examined by Nebgen and Lowe (1982) and Ferguson et al. (1977). These reports conclude that branch angle and branch frequency are weakly to moderately inherited and that only minor genetic gains would result from direct selection for these characteristics because of their limited variation. Further work with mass selection and progeny testing should lead to a more thorough understanding of the potential for genetic improvement of growth rate and crown form in sycamore. The objectives of this study were: (1) to analyze a sycamore progeny test for variation and inheritance of growth rate and branching characteristics, and (2) to estimate expected genetic gains and correlations between traits.

METHODS

Six progeny from each of 48 open-pollinated families representing 5 geographic seed sources were analyzed at the end of the fifth growing season for variation in height and diameter growth rate, percent live crown, branch angle,

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and branch frequency. This progeny test was established by Westvaco Corp. on Island No. 3 in the Mississippi River in Carlisle Co., KY. The test consists of 6 replications of the 48 families planted in 10-tree row plots at a 3.35 x 3.35 m spacing.

Branch angle was measured on all branches in the middle one-third of the crown with a diameter greater than 0.5 cm at the point of insertion. Measurements were made using a large Plexiglas protractor which was marked-off in 10 intervals of 9 degrees. Branch frequency was calculated as the number of measured branches per meter of stem. Live crown was calculated as the percent of total tree height occupied by functional branches.

Analysis of variance employed a nested factorial model with families nested within seed sources. Narrow-sense heritability estimates were calculated for individual trees as:

$$h_I^2 = \frac{4\,\sigma^2_{F(S)}}{\sigma^2_W + \sigma^2_{RF(S)} + \sigma^2_{F(S)}} \tag{1}$$

and for families as:

$$h_F^2 = \frac{\sigma^2_{F(S)}}{\frac{\sigma^2_W}{rn} + \frac{\sigma^2_{RF(S)}}{r} + \sigma^2_{F(S)}} \tag{2}$$

where: $\sigma^2_{F(S)}$ = families within seed source variance

σ^2_W = trees within family variance

$\sigma^2_{RF(S)}$ = replication x family variance

r = number of replications

n = number of trees per plot.

Expected genetic gains and phenotypic and genetic correlations were calculated according to Falconer (1981).

RESULTS AND DISCUSSION

Branch frequency and diameter at breast height were the most variable traits, while total tree height was the least variable (Table 1). Mean values for height and diameter were intermediate to those reported by Nebgen and Lowe (1982) and Ferguson et al. (1977). Branch angle and branch frequency averaged 46 degrees and 6.5 branches per meter, respectively. These values compare favorably with those of Ferguson et al. (1977) for the same traits in 5-year-old sycamore progeny (45 degrees and 6.1 branches per meter, respectively). Nebgen and Lowe (1982) reported a much greater average branch angle (54 degrees) in 7-year-old sycamore.

Table 1.--Means, ranges and coefficients of variation (CV) for growth and crown traits.

Trait	Mean	Individual Tree Range	CV	Family Range	CV
Height (m)	8.08	4.85-10.55	10.76	6.70-9.18	4.70
Diameter (cm)	8.77	3.51-15.60	18.94	6.62-11.19	11.09
Live Crown (%)	75	43-97	13.36	63-86	8.93
Branch Angle (°)	46	30-68	13.35	40-56	7.61
Branch Freq. (br/m)	6.5	2.6-10.8	22.47	4.7-8.3	12.31

All traits differed significantly between families within seed sources (F(S)) (Table 2). Diameter was the only trait which differed significantly between seed sources (S). Significant differences between replications (R) for height, diameter, and live crown and significant interaction effects for height and live crown resulted from microsite variation and possibly non-uniform survival among replications. Mortality among replications ranged from a low of 70 percent to over 91 percent. As a result, sample trees in proximity to one or more non-surviving trees developed under varied degrees of wider spacing. However, this did not influence branch angle or live crown development as a separate analysis indicated that there were no significant differences in live crown or branch angle between trees growing with 0, 1, or 2 non-surviving neighbor trees.

Table 2.--Analysis of variance for growth and crown traits for 5-year-old American sycamore.

Source	d.f.	Mean Square[a]				
		Height	Diameter	Live Crown	Branch Angle	Branch Freq.
S	4	6.84	18.16**	391.42	26.29	2.18
F(S)	43	1.89**	4.83*	265.98*	77.35*	4.43*
R	4	18.89**	21.89**	339.36*	92.69	1.35
R x S	14	2.04*	2.83	112.84	41.37	1.45
R x F(S)	78	.93	2.74	172.48**	42.89	2.68
E	144	.76	2.76	100.37	38.28	2.11

[a] ** significant at $\alpha<0.01$
* significant at $\alpha<0.05$

Variance and covariance components were generated for heritability estimates and correlation coefficients. Expected genetic gains were calculated for two alternative selection strategies. The first was family selection in which the 10 best families out of the total of 48 were selected. The second represented mass selection in which the best 10 trees were selected without regard to family. Selection intensities for these 2 strategies (i=1.38 for family selection and i=2.23 for individual tree selection) were derived from the graphs published by Namkoong and Snyder (1969).

All traits were moderately inherited. Individual tree values were slightly higher than family values (Table 3). The estimates are potentially biased due to the single test location analyzed. Nebgen and Lowe (1982) reported a large range in heritability estimates between test locations and emphasized the need for multiple location testing. However, Webb et al. (1973) suggested that heritability estimates may be adjusted for the lack of genotype x environment interaction by multiplying the estimates by 0.75.

Table 3.--Heritabilities, standard errors, and expected genetic gains for family and individual tree selection.

Trait	$h^2_F \pm SE$	$h^2_I \pm SE$	Family Selection[a]	Individual Tree Selection[b]
			- - - - percent gain	- - - -
Height	.44 ± .16	.51 ± .14	4.0	13.9
Diameter	.41 ± .10	.41 ± .14	5.6	18.2
Live Crown	.35 ± .17	.41 ± .15	4.2	15.0
Branch Angle	.44 ± .15	.49 ± .12	4.7	16.2
Branch Frequency	.40 ± .16	.45 ± .14	7.2	25.4

[a] selection for the best 10 families

[b] selection for the best 10 trees

As a result of their large ranges of variation, branch frequency and diameter exhibited the largest expected genetic gains for both selection strategies. Mass selection of individual trees without regard to family resulted in expected genetic gains which averaged approximately 3.5 times greater than those from family selection. Estimated gains from individual tree selection averaged nearly 18 percent while gains from family selection averaged around 5 percent. The expected genetic gain for branch angle resulting from mass selection (16.2 percent) is twice as great as estimates at similar selection intensities from previous studies. Major reasons for this difference include greater variation in the population than that reported by Nebgen and Lowe (1982) and higher heritability estimates than those of Ferguson et al. (1977). Different methods used to measure branch angle may also have influenced these values.

To analyze the relationship between growth rate and crown form, phenotypic and genetic correlation coefficients were calculated (Table 4). Due to the high standard errors usually associated with genetic correlation coefficients (Goggans 1964), statistical significance levels have been determined solely for the phenotypic values.

Statistically significant phenotypic correlation coefficients indicated a negative relationship between live crown and both height and diameter growth rate. However, the respective genetic correlations showed that trees with greater growth rates had larger live crowns, the genetic relationship between live crown and diameter was particularly strong (0.68). The environmental component of the phenotypic correlation coefficients probably confounded that relationship.

Table 4.--Phenotypic[a] and genetic correlation coefficients among growth and crown traits[b].

	Height	Live Crown	Branch Angle	Branch Frequency
Diameter	.74(.79**)[c]	.68(-.12*)	-.28(-.10)	.08(.05)
Height		.12(-.14*)	.07(-.09)	-.23(-.07)
Live Crown			-.48(.13)	-.36(-.21**)
Branch Angle				-.42(-.02)

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[a] phenotypic correlations in parentheses

[b] significance determined for phenotypic values only

[c] ** significant at $\alpha<0.01$
  * significant at $\alpha<0.05$

The negative correlation between live crown and branch frequency suggested that trees with larger live crowns had fewer productive branches per meter of stem than smaller live crowns. Genetic correlations also indicated that direct selection for diameter growth rate would result in trees with larger live crowns and more acute branch angles. These findings are in accordance with those of Nelson et al. (1979), who predicted that the fast-growing cellulose-producing tree of the future would have much larger crowns with a more fastigate form than has been tolerated in the past. Changing objectives from short-rotation fiber production to longer rotation sawlog or veneer log production may require some sacrifice in growth rate as selection is made for flatter branch angles, lower branch frequency and reduced live crown.

CONCLUSIONS

(1) Significant variation existed among families for all growth and crown traits studied to reward a breeding program based upon family selection. Diameter growth rate was the only trait which could be improved through selection from broad geographic seed sources in our study.

(2) All traits were moderately inherited. Average genetic gains approaching 18 percent are possible if mass selection is made for the best 10 trees without regard to family. These gains are approximately 3.5 times larger than potential gains resulting from family selection.

(3) Selection for flatter branch angles to potentially improve wood quality may not be advisable due to a correlated reduction in diameter growth rate. Selection for fewer branches would result in increased height growth and flatter branch angles.

(4) If the primary objective is wood fiber production, selection should be made to increase diameter growth rate. The resulting trees will have more fastigate crowns and persistent live branches.

LITERATURE CITED

Falconer, D. S. 1981. Introduction to Quantitative Genetics. 2nd ed. Longman Inc., New York. 340 pp.

Ferguson, R. B., S. B. Land, Jr., and D. T. Cooper. 1977. Inheritance of growth and crown characteristics in American sycamore. Sil. Genet. 26(5-6):180-182.

Goggans, J. F. 1964. Correlation and heritability of certain wood properties in Loblolly pine (Pinus taeda L.). Tappi 47(6):318-322.

Larson, P. E. 1962. A biological approach to wood quality. Tappi 45(6):443-448.

Namkoong, G., and E. B. Snyder. 1969. Accurate values for selection intensities. Sil. Genet. 18(5-6):172-173.

Nebgen, R. J., and W. J. Lowe. 1982. Inheritance of growth, branch angle, and specific gravity in three American sycamore populations. Sil. Genet. 31(2-3): 86-89.

Nelson, N. D., T. Burk, J. G. Isebrands, and A. R. Ek. 1979. Clone and spacing effects on branch characteristics of short-rotation-intensively-cultured Populus. Proc. 1st N. Cent. Tree Improv. Conf. pp. 74-85.

Webb, C. D., R. P. Belanger, and R. G. McAlpine. 1973. Family differences in early growth and wood specific gravity of American sycamore (Platanus occidentalis L.). Proc. 12th Southeast. For. Tree Improv. Conf. pp. 213-227.

ESTIMATION OF GAIN IN FORM, QUALITY AND VOLUMETRIC TRAITS OF AMERICAN SYCAMORE IN RESPONSE TO THE SELECTION FOR TREE DRY WEIGHT

Barbara G. McCutchan[1]

Abstract.--The genetic relationship of tree dry weight to form, quality and volumetric traits of American sycamore (Platanus occidentalis L.) was obtained from 1080 open-pollinated eight-year-old trees measured for DBH, height, straightness and crown score and from 233 trees measured for tree dry weight, specific gravity and moisture content. Tree dry weight is positively correlated with taller (r_G = 0.94), larger (r_G = 0.99), straighter trees and with better crown configuration, lower moisture content and higher specific gravity. Selection for tree dry weight is estimated to improve tree dry weight 23.9 percent from roguing first generation seed orchards and 42.9 percent from establishing second generation seed orchards. Selection pressure should be placed on total height to achieve optimum amounts of gain for tree dry weight in combination with other desirable traits.

Additional keywords: Platanus occidentalis L., heritability, genetic correlation, expected gain, correlated response.

INTRODUCTION

Selection criteria for tree improvement need to be flexible to the multiple uses of a species. American sycamore (Platanus occidentalis L.) has rapid juvenile growth, is amendable to plantation cultural practices (Steinbeck et al. 1972) and tree improvement programs, and is suitable for a variety of products: veneer, sawtimber, energy and pulpwood (Merz 1958, McElwee et al. 1970, Panshin and deZeeuw 1980, Steinbeck et al. 1972). Whole tree chips are utilized for energy and pulp uses, whereas only the stemwood is suited for timber purposes. If the ratio of stem-to-total tree dry weight is essentially the same for all trees, then a selection criterion for improvement common to each of these uses is increased dry weight of the tree. Other characteristics important for the particular uses are: stem straightness and taper for veneer; straightness, high density and low fibril angle for sawtimber; dry weight per unit volume for energy (Goldstein 1979); and high cellulose content, long fibers and fiber flexibility for pulp yield, tear strength and burst and tensile strength (Amidon 1981). Specific gravity, an easily measured trait, is positively correlated with the proportion of fibrous and ray tissues and with thick walled fibers (r = 0.78) and negatively correlated with vessel volume (Taylor 1969). A measure of specific gravity will indicate the density of the wood (important for energy and sawtimber) but not the particular microscopic traits that determine the quality of the pulp for different uses.

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This paper addresses the following objectives through the examination of an open-pollinated progeny test: (1) evaluate the correlated response in volumetric, form and wood morphological traits resulting from direct selection for tree dry weight and (2) assess trait(s) on which selection should be placed to achieve an increase in tree dry weight in a practical breeding situation.

MATERIALS AND METHODOLOGY

An eight-year-old open-pollinated American sycamore progeny test, belonging to the North Carolina Forest Service, was the data base for this study. The 30 parent trees were selected in natural stands in western North and South Carolina (Figure 1) according to the North Carolina State University Hardwood Cooperative selection criteria of crown configuration, straightness, pruning, branch angle and epicormic sprouting (Purnell and Kellison 1983). These trees were grafted into a first generation seed orchard located in Morganton, North Carolina. Open-pollinated seed of the parent trees, collected from ortets, was the source of a progeny test established adjacent to the Catawba River in McDowell County, North Carolina.

The progeny test was established in 1973 with 1-0 bare root seedlings on soils of alluvial deposition. Seven replications of ten tree row-plots were randomly planted by family at 3m between rows and 2.4m within rows. Three replications were excluded from the analysis because of inferior tree growth caused by their location on an excessively well drained sand ridge. Survival of the remaining four replications exceeded 90 percent.

After eight years of plantation growth, the North Carolina Forest Service measured all trees in the study for diameter at breast height (DBH), total height, crown configuration score (1 = best to 6 = worst) and straightness score (1 = best to 6 = worse). Following measurement, thinning to five trees per row-plot was prescribed to maintain growth in the closed crown plantation. The marking system was based upon removing inferior trees while maintaining balanced spacing. Two of the trees marked for thinning were used for destructive biomass sampling. Since the thinning was not random, the trees to be destructively sampled were chosen to be as representative as possible in terms of the mean and variance of the row-plot. Some of the ramifications of using this system are dealt with later in this paper; a more detailed account is given by McCutchan (1982).

Field procedures

Two trees per family row-plot per replication (233 trees) were felled at ground level and bucked into quarter lengths to obtain green weight, specific gravity and moisture content for each stem and limb component. Diameter at breast height, total height and live crown length were also recorded. Green weight of each stem quarter section was measured to the nearest 0.05 kg on a portable scale. A 5-cm thick disk sample (wood and bark) was removed at breast, quarter, half and three-quarters heights for estimation of unextracted specific gravity and moisture content (Figure 2). To estimate these traits for the limb wood and bark, a representative limb in each of the low-, middle- and high-crown areas was selected for removal of a 10-cm long disk sample near the middle of the limb. All limbs greater than 0.6cm in diameter were cut off

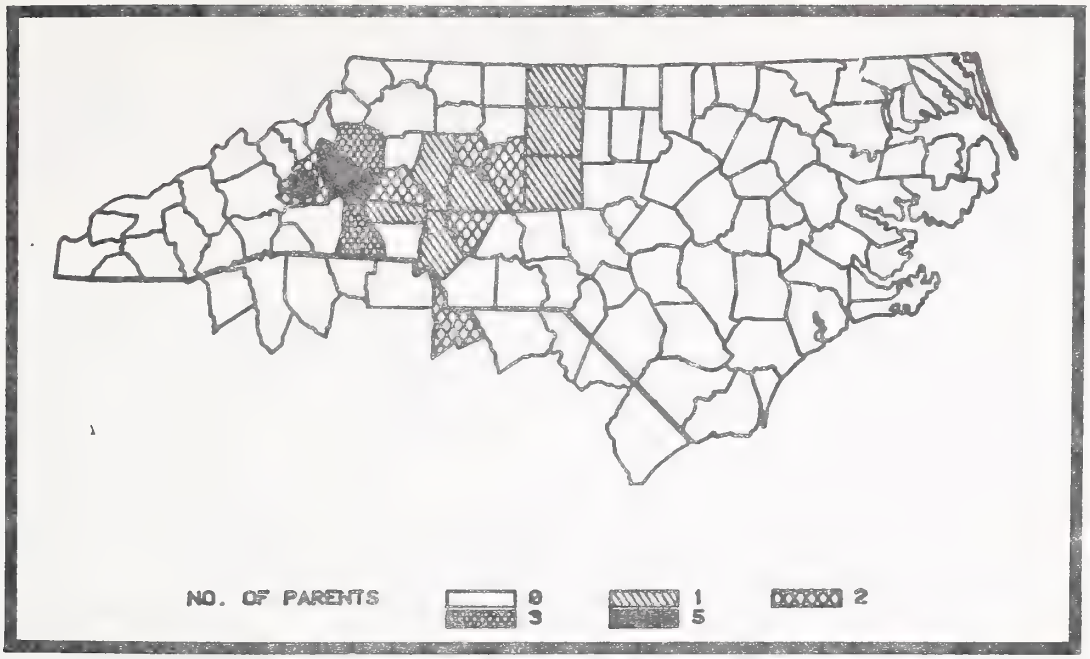

Figure 1.--Distribution of American sycamore parent trees in North Carolina and South Carolina and the progeny test location (indicated by dot).

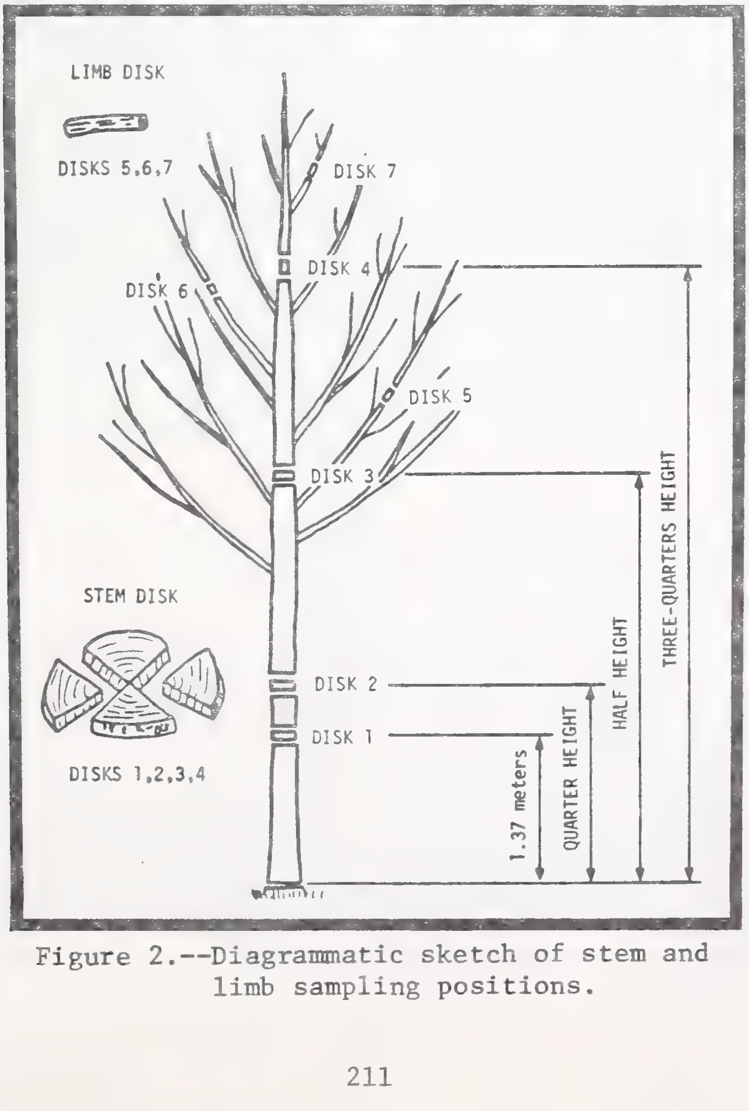

Figure 2.--Diagrammatic sketch of stem and limb sampling positions.

at the junction with the stem and then weighed. The calculation of whole stem specific gravity and moisture content values was based upon an average of sample values weighted by stem volume (Messina et al. 1982); limb values are an average of limb sample values weighted by limb sample radius. Limb and stem dry weights were estimated by applying the estimates of limb and stem moisture content percent to the respective green weights.

Data anlysis

The height, DBH, straightness score and crown score data (1080 observations), and crown length, specific gravity, moisture content and dry weight data (233 observations) were analyzed as a randomized complete block design, examining the random effects of replication, family, replication by family and within plot. Variance components (σ^2_R, σ^2_F, σ^2_{RF} and σ^2, respectively) were estimated for each trait and covariance components were estimated for each trait with tree dry weight, DBH and height. Estimates were obtained using Henderson's Method III for unbalanced data (SAS Varcomp Procedure) (Goodnight 1982). The open-pollinated families were assumed to represent half-sib families; additive genetic variance (σ^2_A) was estimated as four times the family variance component (σ^2_F). Family heritabilities ($h^2_F = \frac{1}{4}\,\sigma^2_A/\sigma^2_{\bar{P}}$, where $\sigma^2_{\bar{P}}$ is the phenotypic variance among open-pollinated family means) and individual-within-family heritabilities ($h^2_W = \frac{3}{4}\,\sigma^2_A/\sigma^2_W$, where $\sigma^2_W = \sigma^2_{RF} + \sigma^2$) were estimated for each trait, as well as the genetic correlation (r_{Gxy}) of each trait "y" with tree dry weight, DBH and height ("x"). Expected genetic gain from direct selection on tree dry weight and the correlated response expected in other traits were estimated for the roguing of the first generation seed orchard (G1[1/]) and for the establishment of a second generation seed orchard (G2 + G3[1/]). Roguing the clonal seed orchard involves only family selection based on progeny test results, whereas the establishment of a second generation seed orchard involves combined selection on family (G2) and individual-within-family (G3) (Namkoong et al. 1966). The calculated expected genetic gain or correlated response in either case does not include the gain from mass selection of parent trees in natural stands.

[1/] where

$$G1 = \left[\sqrt{h^2_{Fx}}\;\sqrt{h^2_{Fy}}\;\sigma_{\bar{P}y}\;r_{Gxy}\;\frac{100\%}{\bar{y}}\;2\right] i_1$$

$$G2 = \left[\sqrt{h^2_{Fx}}\;\sqrt{h^2_{Fy}}\;\sigma_{\bar{P}y}\;r_{Gxy}\;\frac{100\%}{\bar{y}}\right] i_2$$

$$G3 = \left[\sqrt{h^2_{Wx}}\;\sqrt{h^2_{Wy}}\;\sigma_{Wy}\;r_{Gxy}\;\frac{100\%}{\bar{y}}\right] i_3$$

"x" refers to the trait on which direct selection is applied, "y" refers to the trait in which correlated response is expected and i_1, i_2 and i_3 are selection intensities (Becker 1975). When "x" is the same trait as "y", then the gain calculated is expected genetic gain; when "x" differs from "y" then the gain calculated is the correlated response.

RESULTS AND DISCUSSION

The effects of nonrandom sampling were evaluated by comparing the ratio of each gain (G2 and G3) from the trees which had been destructively sampled to the respective gains estimated using all 1080 trees for each DBH and height. Gain due to family selection (G2) for DBH was 10 percent over that estimated using all trees and individual-within-family (G3) was 186 percent higher; for height, G2 was 10 percent higher and G3 was 79 percent higher. To compensate for the overestimated gain, in particular with tree dry weight, tree dry weight was regressed upon DBH^2 x height using an intercept. The predictive equation (tree dry weight in kg/tree = 1.4427 + 0.0169 x DBH^2 x height), with $R^2 = 0.90$, was applied to each tree to estimate its tree dry weight. Variance components and heritabilities were estimated for predicted tree dry weight. The genetic correlations and gain estimates of tree dry weight with other traits is based upon predicted tree dry weight data, where the genetic correlation between predicted tree dry weight and the observed tree dry weight is 0.98. The correlations of predicted tree dry weight with DBH and height includes a correlation of error terms since predicted tree dry weight is a function of DBH squared times height. However, the genetic correlations of DBH and height with predicted tree dry weight in contrast to those with the actual tree dry weight values are the same or less: 0.99 versus 0.99 for DBH and 0.94 versus 1.02 for height.

The mean descriptive statistics for the 30 open-pollinated families are given in Table 1. Mean DBH and height of these eight-year-old trees are similar to the plantation average of five-year-old trees in Mississippi, 9.32 cm and 9.43m, respectively (Tuskan 1980). The mean stem specific gravity, 0.412, was lower than the value 0.43 reported by Tuskan (1980), and lower than the 0.463 value obtained by Lee (1972) for older trees. The stem moisture content of 138.0 percent is slightly higher than that which Tuskan (1980) found, 136.9 percent, and also higher than the value (115 percent) reported by Lee (1972). Eighty-three percent of the mean tree dry weight was in the stem; the comparable ratio of 78 percent was found for Tuskan's five-year-old trees (1980). The amount of variation due to families for the stem-to-tree dry weight ratio and for limb moisture content was nonsignificant at the 5 percent level. All other traits had significant family effects, which indicates that sufficient genetic variation exists to select upon, and were included in subsequent analyses.

Family and individual-within-family heritabilities are listed in Table 2. Family heritabilities for DBH and height agree closely with those found for seven-year-old sycamore of 0.75 and 0.72, respectively (Nebgen and Lowe 1982). Individual-within-family heritabilities for the destructively sampled trees were much higher than for the 1080 trees for both height and DBH, implying that h_W^2 for other destructively sampled traits are higher than if sampling had been random. In addition to sampling problems, additive genetic variance and hence family and individual-within-family heritabilities may be inflated if some of the open-pollinated progeny are full sibs. Inflation may also result from genotype by environment (G x E) variance being confounded with family variance, since the progeny test was established at only one planting site. However, the G x E influence on DBH, height, specific gravity and moisture content may be nonsignificant, inferring from the results of other studies (Land et al. 1983 , Nebgen and Lowe 1982).

Table 1.--Descriptive statistics for mean traits of 30 parents (weighted by the number of progeny)

Trait	Mean	Standard Deviation
Diameter at breast height (cm)	9.72	1.01
Height - total (m)	10.59	0.73
Crown length (m)	6.88	0.90
Live crown ratio	0.65	0.05
Crown score (1 = best, 6 = worst)	3.8	0.5
Straightness score (1 = best, 6 = worst)	3.5	0.5
Limb specific gravity	0.406	0.011
Stem specific gravity	0.412	0.010
Limb moisture content (%)	144.1	6.2
Stem moisture content (%)	138.0	7.4
Limb dry weight (kg/tree)	3.78	1.49
Stem dry weight (kg/tree)	17.57	5.50
Tree dry weight (kg/tree)	21.36	6.87
Predicted tree dry weight (kg/tree)	25.75	5.25
Stem to total tree dry weight (%)	83	2.5

Table 2.--Estimation of family and individual-within-family heritabilities for eight-year-old American sycamore

Traits	Heritabilities	
	Family	Individual-within-family
DBH[a]	0.74	0.26
Height[a]	0.69	0.27
Crown length	0.66	0.85
Live crown ratio	0.46	0.35
Crown score[a]	0.64	0.23
Straightness score[a]	0.68	0.30
Limb specific gravity	0.41	0.30
Stem specific gravity	0.55	0.50
Stem moisture content	0.64	0.89
Limb dry weight	0.45	0.40
Stem dry weight	0.56	0.59
Tree dry weight	0.54	0.56
Predicted tree dry weight[a]	0.74	0.27

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[a] Results based on data from all 1080 trees

Genetic correlation estimates (Table 3) of tree dry weight, DBH and height with other traits show that tree dry weight is positively correlated with other desirable traits. The negative correlations of tree dry weight with crown and straightness score indicate that a better crown and straighter tree is associated with higher tree dry weight. The genetic correlations of height with DBH, height with specific gravity, and DBH with specific gravity confirm Nebgen's (1980) results using seven-year-old sycamore, 0.94, 0.30 and 0.28, respectively. Tree dry weight is most strongly correlated with DBH, height and crown length, the latter being a function of height.

Table 3.--Genetic correlation estimates of eight-year-old plantation grown American sycamore[a]

Trait	Predicted tree dry weight	DBH	Height
DBH	0.99	1.00	0.91
Height	0.94	0.91	1.00
Crown length	0.87	0.89	0.96
Live crown ratio	0.43	0.55	0.64
Crown score	-0.08	-0.18	-0.43
Straightness score	-0.22	-0.29	-0.53
Limb specific gravity	0.49	0.52	0.64
Stem specific gravity	0.28	0.31	0.28
Stem moisture content	-0.08	-0.14	0.11

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[a] Genetic correlations whose absolute values are greater than 0.36 are significantly different from 0.00 at the 5 percent level.

The major objective of this research was to determine the correlated response associated with direct selection for tree dry weight. Those results for roguing the first generation seed orchard (G1) and establishing a second generation seed orchard (G2 + G3) are shown in Table 4. The correlated responses in DBH and height associated with direct selection on dry weight are comparable to expected genetic gains from direct selection on DBH and on height. Better crowns, straighter stems, increased specific gravity and decreased moisture content are expected to be associated with increased tree dry weight.

Practical applications

The proposal for the first generation seed orchard is to rogue the orchard from 30 to 15 parents. For the establishment of a second generation seed orchard the proposal is to select 15 of the 30 parents and to select 2 of the 36 progeny in each of the 15 families. The resulting gains expected in tree dry weight per tree are listed in Table 5. The goal to improve tree dry weight, which is a destructively sampled trait, behooves us to select easily measured traits to use as selection criteria for tree dry weight gain. Diameter at breast height and height are particular traits of interest because of high genetic correlations with tree dry weight, and the ease and common occurrence of DBH and height measurements. The correlated response in tree dry weight for

Table 4.--Coefficient of gain resulting from direct selection on each predicted tree dry weight, DBH and height

Genetic response trait		Direct selection traits		
		Predicted tree dry weight	DBH	Height
Predicted tree dry weight	G1[a]	$30.74i_1$	$30.44i_1$	$28.01i_1$
	G2	$15.37i_2$	$15.22i_2$	$14.01i_2$
	G3	$16.19i_3$	$15.64i_3$	$15.11i_3$
DBH	G1	$15.58i_1$	$15.77i_1$	$13.89i_1$
	G2	$7.79i_2$	$7.89i_2$	$6.94i_2$
	G3	$8.21i_3$	$8.11i_3$	$7.49i_3$
Height	G1	$9.35i_1$	$9.05i_1$	$9.55i_1$
	G2	$4.67i_2$	$4.53i_2$	$4.78i_2$
	G3	$4.92i_3$	$4.65i_3$	$5.15i_3$
Crown length	G1	$16.23i_1$	$16.61i_1$	$17.39i_1$
	G2	$8.12i_2$	$8.30i_2$	$8.70i_2$
	G3	$8.55i_3$	$8.53i_3$	$9.38i_3$
Live crown ratio	G1	$3.85i_1$	$4.93i_1$	$5.46i_1$
	G2	$1.93i_2$	$2.46i_2$	$2.73i_2$
	G3	$2.03i_3$	$2.52i_3$	$2.94i_3$
Crown score	G1	$-1.32i_1$	$-2.93i_1$	$-6.83i_1$
	G2	$-0.66i_2$	$-1.47i_2$	$-3.42i_2$
	G3	$-0.70i_3$	$-1.51i_3$	$-3.68i_3$
Straightness score	G1	$-4.27i_1$	$-5.59i_1$	$-9.83i_1$
	G2	$-2.13i_2$	$-2.80i_2$	$-4.92i_2$
	G3	$-2.25i_3$	$-2.87i_3$	$-5.30i_3$
Limb specific gravity	G1	$1.53i_1$	$1.62i_1$	$1.93i_1$
	G2	$0.76i_2$	$0.81i_2$	$0.96i_2$
	G3	$0.80i_3$	$0.83i_3$	$1.04i_3$
Stem specific gravity	G1	$0.91i_1$	$1.01i_1$	$0.87i_1$
	G2	$0.45i_2$	$0.51i_2$	$0.44i_2$
	G3	$0.48i_3$	$0.52i_3$	$0.47i_3$
Stem moisture content	G1	$-0.62i_1$	$-1.06i_1$	$0.81i_1$
	G2	$-0.31i_2$	$-0.53i_2$	$0.41i_2$
	G3	$-0.32i_3$	$-0.54i_3$	$0.44i_3$

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[a] G1 refers to the percent expected gain from roguing first generation seed orchards; G2 and G3 refer to the expected gain from family and individual-within-family gains, respectively, for establishing second generation seed orchards.

selection on DBH or height are comparable, given the variation that is associated with these estimates. Comparison of these figures can be made in columns two and three of Table 4. Selection for height is expected to result in larger desired gains in crown length, live crown ratio, crown configuration and straightness for both family and within-family selection than if DBH were selected at the same intensities. Less gain in stem specific gravity would be associated with selection for height than with selection for DBH. This situation could be desirable depending upon the type of pulp being made, as Land et al. (1983) points out. Also associated with selection for height would be an increase in moisture content, which is undesirable for any manufacturing process. Moisture content can be manipulated to a greater extent by season of harvest and harvesting technique than can other traits (Land et al. 1983), reducing the seriousness of the positive (nonsignificant) correlation of height and moisture content.

Table 5.--Expected genetic gain and correlated responses in tree dry weight when selecting on tree dry weight, DBH and height

Genetic response trait	Direct selection traits					
	Predicted tree dry weight (%)		DBH (%)		Height (%)	
Predicted tree dry weight	G1=23.88 G2=11.94 G3=30.95	42.89	G1=23.65 G2=11.82 G3=29.89	41.71	G1=21.77 G2=10.88 G3=28.88	39.76

Another factor which has bearing in choosing between height and DBH is whether or not the half-sib assumption is valid. If there were full-sibs in the open-pollinated families, then there would be some dominance variance in the family variance component; gain estimates would be inflated. No information on the amount of dominance variance in DBH or height is available for sycamore, but for loblolly pine, there is a larger proportion of dominance variance in the full-sib family variance component for basal area than there is for height (Stonecypher et al., 1973). If there is a larger proportion of dominance variance in DBH for sycamore compared to height, then selection for roguing the first generation seed orchard and for establishing the second generation seed orchard should be on height. If the half-sib assumption is valid, then we can select upon either DBH or height to improve tree dry weight. Given the possible failure of the half-sib assumption and the higher correlated response generally associated with selection for height, selection in both the roguing of the first generation seed orchard and for establishment of the second seed orchard should be for height.

CONCLUSIONS

The evaluation of 1080 trees for DBH, height, straightness and crown score and a subset of 233 trees for tree dry weight, specific gravity and moisture content has elucidated the relationships of tree dry weight with the other aforementioned traits. Tree dry weight is positively correlated with taller, larger, straighter trees with better crown configuration, lower moisture content and higher specific gravity. Selection for tree dry weight is estimated to result in 23.9 percent improvement in tree dry weight from roguing first generation seed orchards and 42.9 percent improvement from establishing second generation seed orchards. Selection pressure should be placed on total height to achieve optimum amounts of gain for tree dry weight in combination with other desirable traits.

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LITERATURE CITED

Amidon, T. E. 1981. Effect of the wood properties of hardwoods on kraft paper properties. TAPPI 64(3):123-126.

Becker, W. A. 1975. Manual of Quantitative Genetics. Third Edition, Wash. State Univ. Press, Pullman, WA, 170 pp.

Goldstein, I. S. 1979. Energy sources derivable from wood on an industrial scale for individual, communal and manufacturing applications. A special report for FAO Forestry Depart. 42 pp.

Goodnight, J. H. 1982. Varcomp Procedure. In: SAS User's Guide: Statistics. 1982 Edition. A. A. Ray, Editor. SAS Institute Inc., Cary, NC 584 pp.

Land, S. B., Jr., S. G. Dicke, G. A. Tuskan and P. E. Patterson. 1983. Genetic, site and within-tree variation in specific gravity and moisture content of young sycamore trees. TAPPI 66(3):149-153.

Lee, J. C. 1972. Natural variation in wood properties of American sycamore (Platanus occidentalis L.). Ph.D. Dis. North Carolina State Univ., Raleigh. 113 pp.

McCutchan, B. G. 1982. Estimated gain in form, quality and volumetric traits of American sycamore in response to the selection for tree dry weight. M.S. Thesis, North Carolina State Univ., Raleigh, 82 pp.

McElwee, R. L., R. C. Tobias and A. H. Gregory. 1970. Wood characteristics of three southern hardwood species and their relationship to pulping properties. TAPPI 53(10):1882-1886.

Merz, R. W. 1958. Silvical characteristics of American sycamore. U.S.D.A. For. Serv. Misc. release 26, 20 pp.

Messina, M. G., R. Ballard and D. J. Frederick. 1982. A bole and branch nutrient content sampling scheme for southern bottomland hardwoods. For. Sci. (In press.)

Namkoong, G., E. B. Synder and R. W. Stonecypher. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silvae Genetica 15(3):76-84.

Nebgen, R. J. 1980. Variation in, inheritance of, and correlations between a number of growth and form traits in three sycamore populations. M.S. Thesis. Texas A & M Univ., College Station, Texas. 66 pp.

Nebgen, R. J. and W. J. Lowe. 1982. Inheritance of growth, branch angle, and specific gravity in three American sycamore populations. Silvae Genetica 31 (2-3):86-89.

Panshin, A. J. and C. de Zeeuw. 1980. Textbook of Wood Technology, Fourth Edition. McGraw-Hill Book Co., N.Y. 722 pp.

Purnell, R. C. and R. C. Kellison. 1983. A tree improvement program for southern hardwoods. In: Proc. 17th South. For. Tree Impr. Conf., Univ. of Ga., Athens, 8 pp.

Steinbeck, K., R. G. McAlpine and J. T. May. 1972. Short rotation culture of sycamore: a status report. J. of For. 70:210-213.

Stonecypher, R. W., B. J. Zobel and R. Blair. 1973. Inheritance patterns of loblolly pines from a nonselected natural population. North Carolina Agricultural Experimental Station, Tech. Bull. No. 220, 60 pp.

Taylor, F. W. 1969. Variation of wood properties. For Prod. Util. Lab., Miss. State Univ. State College, MS., Research Report No. 7. 18 pp.

Tuskan, G. A. 1980. Genetic variation and prediction equations for biomass components in plantation-grown American sycamore. M.S. Thesis. Miss. State Univ., MS. 78 pp.

GENETIC VARIATION OF SIX-YEAR-OLD OPEN-POLLINATED PROGENY OF SWEET PECAN TREES

John R. Toliver and Furcy J. Zeringue II[1]

Abstract.--Open-pollinated progenies from the 10 best phenotypes within each of 4 localized stands of pecan were grown in plantations at two different locations. Five years after outplanting, the trees on a well-drained upland site were significantly taller and had 30% greater survival than the progenies on a moderately-drained bottomland site. Family-within-stand variation was found to be significant for height and survival but there was no variation among stands nor were there genotype-by-environment interactions ($p < .05$). Individual tree heritability for height was .17 and family heritability was 0.48. By selecting the best four families realized gain was 29% for height and 5% for survival. Phenotypic selection of the best trees was found to be of no value when the selected progeny were compared to progeny of unselected trees within the stands.

Additional keywords: *Carya illinoensis*, genetic gains, half-sib families, heritability, phenotypic selection.

Sweet pecan (*Carya illinoensis* (Wangenh.) K. Koch) is well known for its sweet nut meat and high quality wood. Although successful genetic selection for nut quality and production has been attained for many years in the South, little attention has been given to genetic improvement for wood production. In the mid-1950's, demand for high quality pecan logs increased (Adams and Thielges 1974) and this plus the clearing of much of the bottomland hardwood sites where pecan naturally occurs has led to a decrease in supply.

Pecan is most commonly found and grows best on well-drained, loamy soils along river-front ridges and flats (Fowells 1965). The existence of many acres of sweet pecan orchards throughout the South indicates that the species can be grown under intensive culture and on a wide variety of sites. Pecan can be important to landowners as they can establish plantations of trees at relatively close spacings to produce high-quality veneer logs and perhaps take advantage of the income of annual nut crops. Thus, it appears to be a good species for planting and the selection of genotypes capable of rapid growth and good form is important.

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This study was initiated to investigate the source and degree of genetic variation among stands and half-sib families of sweet pecan. It was also designed to determine the efficiency of moderate phenotypic selection of individual trees or stands and selection by progeny testing (Adams 1976).

METHODS

Four relatively pure stands (groups) of pecan trees were located within a mixed bottomland hardwood forest on Raccourci Island near the Mississippi River in south-central Louisiana. These stands were approximately two acres in size and from 0.5 to 5 miles apart. Within each of these stands the ten best parent trees were selected based on their superior phenotypic appearance relative to neighboring trees. Selection of the best trees was based on apparent vigorous growth, position of the crown (dominant or codominant), straightness of bole, absence of limbs for at least 10-15 meters of the bole length and a full, live crown for at least one-third of the total height of the tree (Adams 1976).

Open-pollinated seed were collected from each selected tree and kept separated. In addition, seed were collected and composited from other unselected pecan trees within each stand. These four composited collections were used as check seed-lots against the selected trees from within their respective stands (Adams 1976).

The seed were stratified and planted in a nursery in the Spring of 1974. The resulting 1-0 half-sib seedlings were planted in the Spring of 1975 at two locations. One test was planted on Bass Pecan Company property near Lumberton, Mississippi. The soil at this site is a mature, loamy, well-drained soil previously occupied by longleaf pine (Pinus palustris Mill.). The second test was planted on an old field located near Baton Rouge, Louisiana. The soil is a relatively young, heavy clay, moderately-drained alluvial soil of the Mississippi River flood plain.

Both plantations were laid out in a randomized block design, each consisting of four replications. Included at random within each replication were 40 half-sib families (4 stands, 10 families per stand) and the 4 composited seed-lots, with each represented by single row plots of 5 seedlings. The seedlings were planted on a 3 m x 3 m spacing.

After 5 years of growth in the field, height of the half-sib trees was measured and survival was calculated. The Statistical Analysis System (SAS) procedure GLM (General Linear Model) as described by Ray et al. (1982) was used to perform the analysis of variance. SAS procedure VARCOMP was used to compute the variance components to estimate heritability.

RESULTS AND DISCUSSION

Plantation Performance

Mean height and survival of the trees in the five-year-old plantation were 97 cm and 79%, respectively. Height and survival were significantly superior at the Lumberton, Mississippi, site (Table 1). Climatic conditions at both plantations were very similar. However, the two sites were quite different in terms of soil fertility, soil structure, and soil texture with the Baton Rouge site appearing to be the more favorable according to soils analyses (Sparks 1977).

Table 1. Overall means of height and survival of six-year-old half-sib pecan trees grown at two locations.[1]

Location	Height (cm)	Survival (%)
Lumberton, MS	113	95
Baton Rouge, LA	76	65

[1] Means of both variables are significantly different ($p < 0.05$).

The superior performance of the seedlings located on the Lumberton upland site over the Baton Rouge bottomland site is thought to be the result of at least two factors. Soil at the Lumberton site was classified as a well-drained loam to sandy-loam soil, whereas the Baton Rouge soil was classified as a moderately-drained, silty-clay-loam to clay soil. Root systems of the trees at Lumberton probably grew and developed more rapidly and extensively, thus promoting early growth. Also, while not measured, weed competition appeared to be more intense at the Baton Rouge site even though both plantations were mowed or disked 2-3 times per year for the first three years (Sparks and Toliver 1978).

The superior growth and survival of the trees at the Lumberton site was evident when the trees were two years old. At that time, it was thought that eventually the trees would better utilize the more fertile bottomland site at Baton Rouge and equal or surpass those at Lumberton (Sparks 1977, Sparks and Toliver 1978). However, the differences increased with 3 years of additional growth. At age 2 years, there was a difference of 11 cm (41% taller) in height and 14% in survival (Sparks and Toliver 1978). At age 6 years, these differences were 37 cm (49% taller) in height and 30% in survival. Thus, the Lumberton site was the better site and the growth and survival differences between the two sites had increased.

Genetic Variation

Among the potential sources of genetic variation, only differences among the selected half-sib families within stands were found to be significant for height and survival (Table 2). No significant differences were found among stands, implying that the four subpopulations were not genetically different for height growth or survival. Therefore, more gentic diversity exists among individual trees within the stands than among groups of trees or stands within the forest. This is not surprising when one considers the closeness of the stands to each other and the fact that pecan is wind pollinated. Single tree differences are common among forest trees and the location of Raccourci Island along the Mississippi River could enhance such genetic diversity. Seed could be carried great distances down-river by water. Thus, it is possible for some parent trees on the Island to be from different genetic populations but the population as a whole should be fairly homogeneous.

Table 2. Analysis of variance for height and survival after the fifth season of growth for half-sib families of pecan grown at two locations.

Source of Variation	df(ht)	MS(ht)	df(surv)	MS(surv)
Locations	1	345685.55*	1	25.10*
Reps(Locations)	6	31782.59*	6	2.37**
Stands	3	3111.84	3	0.12
Locations x Stands	3	5723.58	3	0.09
Families (Stands)	35	5546.59**	35	0.26**
Locations x Families (Stands)	30	2057.26	30	0.17
Error	1040	2024.82	1341	0.13

*p < 0.05; **p < 0.01

Neither the location by stand nor location by family -within-stand interactions were found to be significant. Thus, a genotype-by-environment interaction was not evident and it is assumed that the family performances are relatively the same at both plantations.

Phenotypic Selection versus Genetic Selection

One objective of this study was to determine if collection of seed from good phenotypes within a stand would result in a gain in growth and quality of the progeny. In all four stands, the mean height of the progeny of the selected trees was less than the mean height of the progeny from the seed collected from the unselected trees (Table 3). Mean survival was also greater except in stand 1. The overall mean height of the unselected progeny was 108 cm versus 97 cm for the selects (a significant difference) and survival was 81% vs. 79%, respectively. Thus, phenotypic selection was not successful and seed could easily be collected and composited from any group of pecan trees on the Island without loss of growth or survival.

Table 3. Means of height and survival for six-year-old pecan trees grown on two sites.

Progeny from:		Ht(cm)		Survival(%)
All trees (selected and unselected		98		79
All selects		97	**	79
All unselected		108		81
Stand 1	(selects)	97		80
	(unselected)	110		70
Stand 2	(selects)	93		77
	(unselected)	108		85
Stand 3	(selects)	91		77
	(unselected)	103		88
Stand 4	(selects)	104		80
	(unselected)	113		82

**Significantly different ($p < .01$).

On the other hand, genetic selection through progeny testing has potential for substantial gain. Heritability estimates for height were 0.48 for family heritability and 0.17 for single tree heritability based on the half-sib progeny of the selected trees. If these heritabilities hold and the range in heights as shown in Table 4 is maintained or increased, then gain in height could be achieved.

If one were to select the best 4 families (top 10%) based on height, then families 2-1, 4-8, 1-3, and 4-4 would be chosen (Table 4). Realized gain over the population means would be 28 cm (29%) in height and 5% in survival at age six years. Even a lower intensity of selection such as the best 10 (top 25%) would yield a gain of 18 cm (18%) in height and 1% in survival. Thus, selection through progeny testing should be successful in improving height growth and survival of pecan.

Table 4. Means of height and survival of 6-year-old half-sib families of pecan.

Stand-Family	Ht(cm)	Survival(%)	Stand-Family	Ht(cm)	Survival(%)
1-1	104	86	2-1	130	82
1-2	83	88	2-2	73	80
1-3	125	85	2-3	86	55
1-4	80	68	2-4	84	80
1-5	102	85	2-5	79	82
1-6	55	35	2-6	108	75
1-7	90	80	2-7	77	65
1-8	103	75	2-8	78	77
1-9	97	92	2-9	---	---
1-10	89	84	2-10	113	82
Stand 1 mean	97	80	Stand 2 mean	93	77
1-U	110	70	2-U	108	85
3-1	80	78	4-1	100	92
3-2	99	92	4-2	94	92
3-3	97	85	4-3	99	68
3-4	70	72	4-4	123	78
3-5	84	53	4-5	87	72
3-6	74	50	4-6	84	82
3-7	85	85	4-7	109	83
3-8	104	74	4-8	127	70
3-9	101	70	4-9	116	88
3-10	95	85	4-10	101	80
Stand 3 mean	91	77	Stand 4 mean	104	80
3-U	103	88	4-U	113	82

U: Unselected composited check.

CONCLUSIONS

After six years of growth, half-sib families of pecan trees grew better on a well-drained upland site than on a moderately-drained bottomland site. Heavy weed competition on the bottomland site probably contributed to the poorer survival and growth of the trees.

Collection of seed from the best phenotypes within a stand did not result in a gain in height or survival over seedlings grown from seed collected from the unselected trees in a stand.

Family-within-stand variation in height and diameter was highly significant and considerable gain can be made by selecting the best families. No significant differences were found among stands and there was no evidence of genotype-by-environment interactions.

Based on data of six-year-old progeny of trees selected from a localized population of pecan, progeny testing must be performed in order to obtain improvement in height and survival of pecan trees.

LITERATURE CITED

Adams, J.C. 1976. A study of genetic variability in wild populations of pecan (Carya illinoensis (Wangenh.) K. Koch). Ph.D. dissertation, Louisiana State University, Baton Rouge, La. 111 p.

Adams, J.C. and B.A. Thielges. 1974. Genetic improvement of pecan for wood production. Proc. 9th Central States Tree Improvement Conference. p. 159-163.

Fowells, H.A., ed. 1965. Silvics of forest trees of the United States. USDA Agric. Handb. No. 271. 762 p.

Ray, A.A., ed. 1982. SAS user's guide: statistics. 1982 edition. SAS Institute, Inc., Cary, N.C. 584 p.

Sparks, R.C. 1977. Performance of three-year-old open-pollinated progeny of selected pecan (Carya illinoensis (Wangenh.) K. Koch) trees. M.S. thesis, Louisiana State University, Baton Rouge, La. 68 p.

Sparks, R.C. and J.R. Toliver. 1978. Natural variation in a wild population of pecan. Proc. Louisiana Academy of Sciences. Vol. XLI. p. 57-62.

GEOGRAPHIC VARIABILITY IN GROWTH OF TEN-YEAR-OLD GREEN ASH FAMILIES WITHIN EAST TEXAS

A. F. Stauder, III[1] and W. J. Lowe[2]

Abstract.--Open-pollinated progeny from 58 green ash selections in East Texas representing 15 counties were planted at three locations within East Texas. Seedlings representing five geographic areas in East Texas were planted in two locations, Northeast Texas and Southeast Texas. Survival was excellent across the five plantations, ranging from 95 to 98 percent with an average of 97 percent. Average volume estimates ranged from 6.6 dm^3 per tree to 17.5 dm^3 per tree across the plantings and averaged 10.0 dm^3 per tree. There were no significant differences for the variables measured due to the geographic area of seed collection within East Texas. The planting location effect was highly significant for height, diameter, and volume. The planting location by family interaction was significant only for survival and volume. Heritability estimates ranged from $h^2 = .51$ for volume to $h^2 = .66$ for height and diameter. Volume per tree can be increased about 1.40 dm^3 by selecting the ten best families in the combined analysis.

Additional keywords: Fraxinus pennsylvanica, progeny tests, heritability.

Green ash (Fraxinus pennsylvanica Marsh.) is a bottomland species and is the most widely distributed species of American ash (Harlow and Harrar 1969). The range of green ash extends from the East Coast of the United States and Canada westward into eastern Texas in the South, and eastern Alberta, Canada in the North. Its moderately high wood specific gravity and low wood moisture content make green ash a high valued species for solid wood products as well as for pulp and paper (Talbert and Heeren 1979). Both the North Carolina State University-Industry Hardwood Research Cooperative and the Western Gulf Forest Tree Improvement Program-Hardwood have active tree improvement programs underway with green ash and selected trees have been accepted for use in seed orchards and breeding arboretums (North Carolina State University 1982, Byram et al. 1982). Even though green ash performs best on moist bottomland sites, it is unusually versatile in site requirements and once established, will persist on droughty sterile soils.

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METHODS

Open-pollinated seed from 58 green ash selections in East Texas representing 15 counties were collected in 1968 and 1970 (figure 1). The seedlings from these selections were grown in 1971 in three replications at Indian Mound Nursery located near Alto, Texas. Three progeny tests were established in early spring 1972: 1) Harrison County, 2) Burleson County, and 3) Montgomery County. Seedlings representing seven geographic areas of seed collection in East Texas were planted at two locations in East Texas, Harrison County and Montgomery County. Because of insufficient representation from two of the areas, data from only five areas were used in the analysis. These provenance studies were planted adjacent to the progeny tests. With the exception of the test at Burleson County which was four replications, the field design was a six-replicate, randomized complete block with four-tree-row family plots. Spacing was 10 by 10 feet in each planting. A single border row was used at each location to offset edge effects. All seedlings were root-pruned to eight inches and top-pruned to a height of five inches.

The Harrison County planting was cleared previously forested land of silty loam soil. The Burleson County plot was alluvial soil of the Brazos River which had been under intensive agriculture for many years. The planting at Montgomery County was an old forested area previously planted in a plantation which was abandoned one year after planting. All sites were disced prior to planting.

Weeds and sprouts were controlled in all tests by discing during the first three years and mowing thereafter. Chemical weed control was used at the Burleson County planting. The four tests at Harrison and Montgomery Counties were fertilized in 1973 and 1974 respectively.

Provenance and family variation were examined by a least squares regression approach using the General Linear Model (GLM) procedure of Statistical Analysis Systems (SAS) (Barr et al. 1979). Plot means were used in each of the combined analyses. The geographic area of seed collection was considered as a fixed effect, while locations, replications and families were considered as random effects. Dead trees were assigned a volume of 0 dm^3 to account for survival differences. A Satterthwaite-F (pseudo-F) test was used in the absence of valid tests (Hicks 1973). Family heritability and gain estimates were calculated for height, diameter and volume.

RESULTS AND DISCUSSION

Survival was excellent across the five plantations, ranging from a low of 95 percent at Burleson County to a high of 98 percent at Harrison and Montgomery Counties, and averaging 97 percent at all locations (table 1). At age 10 average plantation height for all plantings was 6.6 meters and diameter averaged 6.9 cm. The planting in Burleson County had the best tree growth while the Montgomery County plantings had the slowest growth.

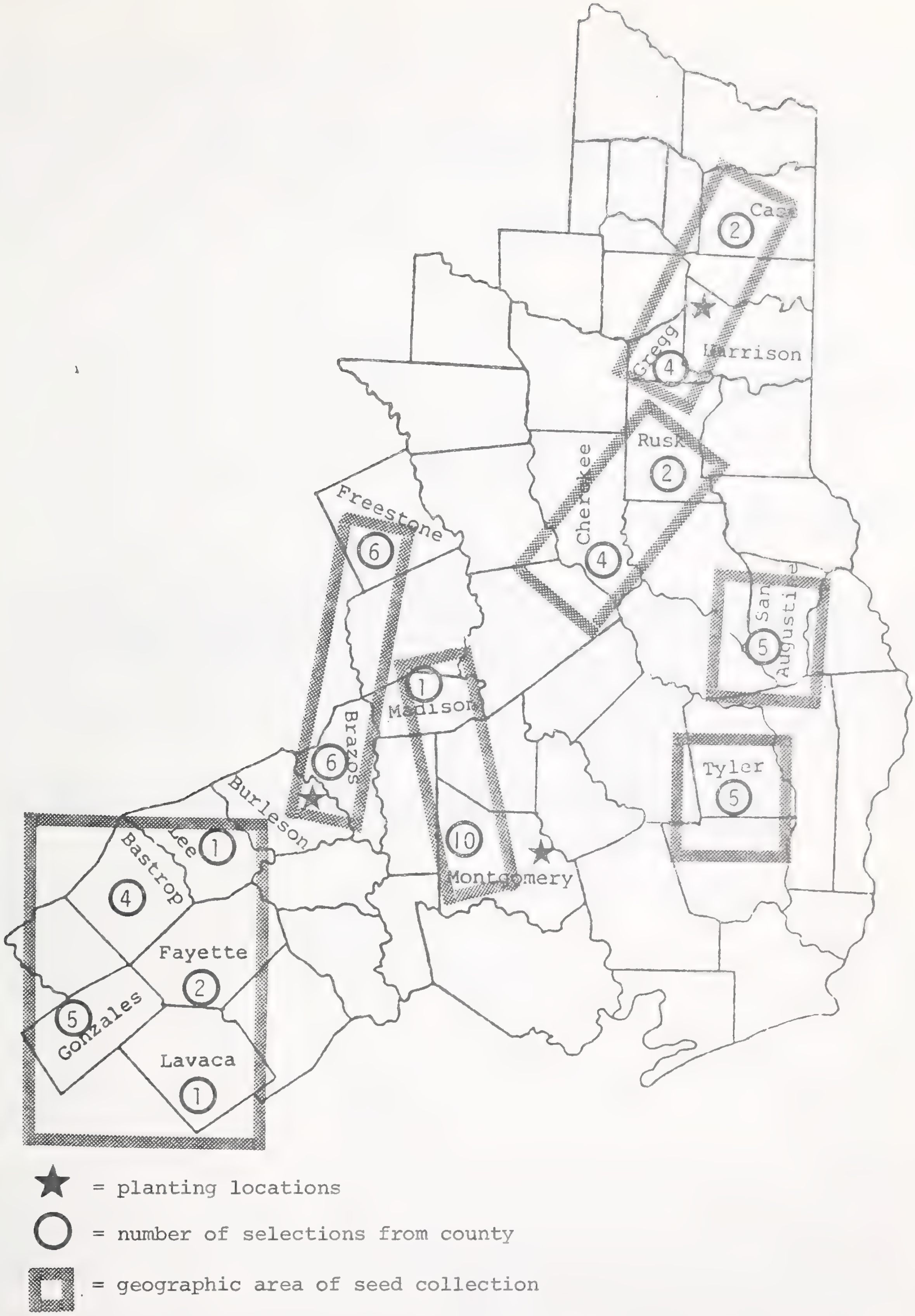

Figure 1. Seed collection locations and plantation locations in East Texas for the 1972 green ash study.

Table 1.--Plantation means for green ash tests at 10 years

Plantation	Survival	Height	Diameter	Volume
	(%)	(m)	(cm)	(dm^3)
Burleson County	95	7.6	9.2	17.5
Harrison County	98	7.1	7.0	10.6
Harrison County (Provenance)	97	6.4	6.5	8.2
Montgomery County	98	5.8	5.8	6.6
Montgomery County (Provenance)	98	6.2	5.8	7.1

Green Ash Provenance Studies

There were no significant differences (0.05 level of significance) for survival, height, diameter or volume growth among the geographic areas of seed collection for the combined analysis (table 2). The planting location by provenance interaction was also non-significant for the measured traits. Therefore, these bulk collection studies indicate that there is not any differences between the sampled geographic areas of seed collection. Green ash seed can be collected from any area within this study's boundaries and planted in East Texas without a loss in survival or growth.

Table 2.--Analysis of variance for survival (Sur.), height (Ht.), diameter, (Dia.), and volume (Vol.) for the combined location provenance green ash analysis

Source of Variation	df	Mean Square for			
		Sur.	Ht.	Dia.	Vol.
Location	1	0.86	2.88	11.06	31.20
Replication (Loc.)	10	24.09	2.47**	2.42**	24.05**
Provenance	4	10.60	1.74	1.72	16.06
Location x Provenance	4	17.88	0.45	0.46	4.36
Error	40	11.72	0.24	0.38	3.48

**significant at the 0.01 level of significance

Green Ash Progeny Tests

An analysis of variance was performed on the data from 42 families that were planted in at least two locations. Location, geographic source, and family effects were included in the model. The provenance and location by provenance terms were non-significant for survival, height, diameter, and volume. This supports the conclusions from the provenance analysis in that there were no significant differences due to the geographic area of seed collection within East Texas.

Because the geographic area of seed collection was non-significant an analysis was performed deleting the provenance effects from the model (table 3). The location effect was non-significant for survival (mean = 97 percent), but was highly significant for height, diameter, and volume. As shown in Table 1 the trees at the Burleson County site were the largest. There were highly significant differences among families for height, diameter, and volume growth, but not for survival. The planting location by family interaction was significant only for survival and volume. The range of family survival was 92 percent to 100 percent, and it is doubtful that this small a difference in survival is important in an operational breeding program.

Table 3.--Analysis of variance of survival (Sur.), height (Ht.), diameter (Dia.) and volume (Vol.) for the combined analysis of three green ash progeny tests

Source of Variation	df	Mean Square for			
		Sur.	Ht.	Dia.	Vol.
Location	2	269.95	146.18**	364.29**	3946.14**
Replication (Loc.)	13	139.28*	8.47**	9.52**	152.73**
Family	41	74.36	3.45**	5.23**	65.12**
Location x Family	66	110.51**	1.17	1.79	32.16**
Error	480	65.35	0.93	1.63	19.12

*significant at 0.05 level of significance
**significant at 0.01 level of significance

Because the planting location by family interaction was highly significant for volume, Spearman Rank correlation coefficients were calculated among the plantings. Correlation coefficients for the Burleson County planting with the plantings at Harrison County and Montgomery County were not significant (0.20 and 0.01 respectively). The coefficient between the Harrison and Montgomery County plantings was highly significant (r = 0.56), indicating that much more consistent family rankings occurred between these two plantings. One reason for the differences in family rankings may be because the Burleson County planting was previously under intensive agriculture, while the other plantings were previously forested land. The Burleson County planting also contained the fewest number of families. Selected families performed well at all three planting locations and a breeding program can be developed utilizing these families. The need for multi-location testing is stressed however, because of the significant family by planting location interaction for volume growth.

Family heritability and gain estimates were calculated for height, diameter, and volume (table 4). These indicate that these traits are strongly inherited in green ash. Estimates ranged from $h^2 = .51$ for volume to $h^2 = .66$ for both height and diameter. Gain in growth traits by selecting the best ten families out of 42 for height, diameter, and volume were 0.33 m (5 percent), 0.48 cm (6 percent), and 1.40 dm^3 (12 percent) respectively. These gains for growth traits appear to be large enough for use in a tree improvement program.

Table 4.--Family heritabilities (h^2), standard error (SE) of heritability, and estimated genetic gains for the combined analysis of three green ash progeny tests

Variable	Family h^2	SE h^2	Gain
Height	0.66	0.22	0.33 m
Diameter	0.66	0.22	0.48 cm
Volume	0.51	0.21	1.40 dm^3

CONCLUSIONS

The geographic area of seed collection within East Texas had no effect on survival or growth; therefore, green ash seed can be collected from any area within the boundaries of this study and planted in East Texas without a loss in survival or growth. Family differences were important in height, diameter and volume growth but not for survival. The planting location by family interaction was highly significant for survival and volume. Well adapted families can be identified with multiple location testing. Growth traits appear to be strongly inherited in green ash (height and diameter $h^2 = 0.66$, volume $h^2 = 0.51$). By selecting the 10 best families expected genetic gains were 5 percent for height, 6 percent for diameter, and 12 percent for volume growth.

LITERATURE CITED

Barr, A. H., J. H. Goodnight, J. P. Sall, W. H. Blair and D. M. Chilko. 1979. SAS User's Guide, 1979 ed. SAS Institute, Inc., Cary, NC. 494 p.

Byram, T. D., W. J. Lowe, C. R. McKinley, J. F. Robinson, A. Stauder and J. P. van Buijtenen. 1982. 30th Progress Report of the Cooperative Forest Tree Improvement Program. Forest Genetics Lab, Texas Forest Service Circular 262. 25 p.

Harlow, W. M. and E. S. Harrar. 1969. Textbook of Dendrology. McGraw-Hill Book Co., New York. 512 p.

Hicks, C. R. 1973. Fundamental concepts in the design of experiments. Holt, Rinehart and Winston. New York. 349 p.

North Carolina Sate University. 1982. Nineteen annual report, N.C. State University-Industry Cooperative Hardwood Research Program. Sch. Forest Resor., Raleigh, NC. 53 p.

Talbert, J. T. and R. D. Heeren. 1979. Sex differences in green ash. South. Jour. of Appl. For. 3(4):173-174.

GEOGRAPHIC PATTERNS OF VARIATION AMONG SWEETGUM POPULATIONS IN THE SOUTHERN UNITED STATES--FOURTEENTH-YEAR RESULTS

George W. Stubblefield[1]

Abstract.--Open-pollinated seeds were collected from 5 trees in 2 stands located in 14 geographic sources across the southern United States. A subsample of trees from 6 of the 14 geographic sources plus a common set of check lots, one from each of the 14 sources, were planted at 7 locations. The patterns of geographic variation among sources, stands, and trees for height and DBH were analyzed using analysis of variance. Differences among families/stands/geographic source were highly significant (.01 level) at 5 of 7 plantings for height and DBH. Variation among stands/geographic source was not significant at any planting. Variation among geographic sources was significant at only 2 plantings. Coastal Plain sources tended to grow better than Piedmont sources at Coastal Plain or bottomland sites. Piedmont sources were generally better on Piedmont sites.

Additional keywords: *Liquidambar styraciflua* L., provenance variation.

INTRODUCTION

One function of a species provenance study is to determine the geographic patterns of variability of economically important traits. Geographic differences are expected for species that are found over large areas. Previous studies have found significant geographic variation in sweetgum (*Liquidambar styraciflua* L.) (Webb 1964; Ferguson and Cooper, 1977; Wells *et al.*, 1979). Because the amount of genetic variation in a breeding population affects genetic gain, provenance studies are an appropriate first step in an intensive tree breeding program. Provenance studies can also indicate the best sources for specific locations and guide the movement of seed sources between locations.

MATERIALS AND METHODS

Seed Collection

The Rangewide Sweetgum Provenance Study was initiated in 1964 by the North Carolina State University - Industry Hardwood Research Cooperative.

Seven transects were drawn to cover the range of sweetgum in the southern United States (Figure 1). Transects ranged from North Carolina (1) to Texas (7) and coincided with lands of members of the N. C. State Hardwood Cooperative. Each transect traversed two physiographic regions creating 7 transects by 2 regions or 14 geographic sources. Transects 1 to 4 covered Coastal Plain (designated A) and Piedmont (B) provinces. Transect 5 compares lower Coastal Plain (A) and upper Coastal Plain (B) provinces. Transect 6 compares Mississippi riverbottom (A) and Louisiana upland (B) sites. Transect 7 compares Sabine (A) and Neches (B) river stands. The transect number and letter of the physiographic region designates the geographic source. For example, 5A is a Coastal Plain source of transect 5.

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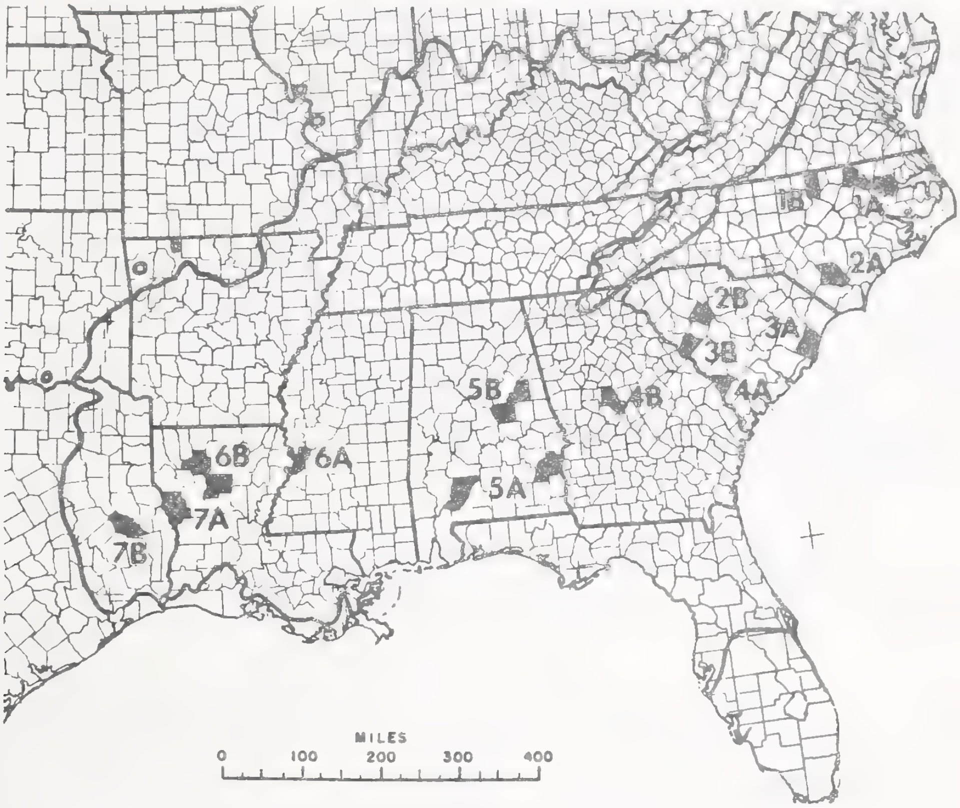

Figure 1.--Location of transects and geographic sources across the natural range of sweetgum.

Two natural sweetgum stands within each of the 14 geographic sources were selected for seed collection. These stands were located on average to good sites.

Open-pollinated seeds were collected from 5 trees in each of the 28 stands. Selection requirements for trees were mild phenotypic superiority, dominance or codominance in their stands, and sufficient quantities of seed for study needs. Selected trees were also separated enough to avoid relatedness through common parentage or similar rootstocks. From the 14 geographic sources X 2 stands/source X 5 families/stand, 140 families were created.

Study Design

Seed collections were made in 1964 and 1965. Seedlings were grown at the North Carolina Forest Service Nursery at Clayton in 1966 at a density of 15 to 20 per square foot. In spring, 1967, seedlings were outplanted onto good sites with one planting located within each area represented by the 14 geographic sources. Each planting of 6 replications was designated by the area representing the geographic sources. For example, planting 3B is located on transect 3 in the Piedmont.

Each of the 14 plantings consists of a check block and a test block. Each check block has 14 check lots, one family representing each of the 14 geographic sources. The same 14 check lots were used at each planting. Check blocks have seedlings from a check lot planted in 3 rows of 12 trees at a 6 X 6 foot spacing.

Each test block consists of 60 families (6 geographic sources X 2 stands/geographic source X 5 families/stand). The 6 geographic sources planted at a location include sources from the transect the study is planted on plus the 2 adjacent transects (Table 1). A planting on transect 4 includes geographic sources from transects 3, 4, and 5. Studies planted on transect 1 include tran-1, 2, and 7. The 60 families at each study site are planted in blocks of 5 families common to a single stand from a geographic source. The 5 family blocks are planted in 12-tree row plots at a 6 X 6 foot spacing.

Table 1.--Occurrence of transects planted in the test blocks at each separate planting.

Transect of planting	Transects included in a test block planting						
	1	2	3	4	5	6	7
1	X	X					X
2	X	X	X				
3		X	X	X			
4			X	X	X		
5				X	X	X	
6					X	X	X
7	X					X	X

Seven of the 14 studies established in 1967 were abandoned by age 10. Growth varied widely between plantings. Mean height at age 14 ranged from 21.6 to 50.2 feet. Thinnings were done in most plantings between ages 6 and 9 years.

Analysis of Results

Only 6 of the 14 plantings have sufficient survival and growth for continued evaluation. These 6 trials were measured at age 14. A seventh study using tenth-year measurements was also included in the analysis. The traits measured in the test blocks were total height (ft.) and DBH (in.). Mean height (ft.) was also determined for the check blocks of the 6 studies measured at age 14.[1/]

Statistical analyses were made using a least squares analysis of variance because data often were unbalanced with occasional missing cells. Not all families had sufficient seedlings for planting needs and were excluded from certain plantings and replications. The PROC GLM option of SAS (Barr *et al.*, 1979) was

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[1/] The studies used were located on lands of Champion-International, Continental Forest Industries, Georgia-Pacific, International Paper, Union-Camp, and Westvaco. Their efforts contributed to this study are appreciated.

used for the analysis of variance. Using coefficients estimated by PROC RANDOM of SAS, mean squares were balanced and approximate F-tests constructed (Satterthwaite 1946). The within-plot error was calculated separately and adjusted by the harmonic mean of trees per plot.

All factors were considered to be random, except for transects. The factors (stands, geographic sources, etc.) constitute a subsample of the larger population of sweetgum. Transects were considered fixed, however, because they were chosen to cover lands of members of the North Carolina State University Hardwood Cooperative to facilitate seed collections.

RESULTS

Results of the least squares analysis of variance are listed in Table 2 for height and DBH for each planting. No combined analysis of all plantings was made because of the overlapping of sources only for adjacent transects (Table 1). Means of tree height and DBH for geographic sources and transects are listed in Table 3. Means for physiographic regions/transects are the same as geographic source means.

Variation among Geographic Sources, Transects, and Physiographic Regions

Significant geographic provenance variation was detected mainly at two plantings (3A and 7A) (Table 2). Height differences were significant at 7A and DBH at 3A.

Despite the variable importance of provenance differences at the seven plantings, certain geographic sources appeared better than others when planted over several sites (Table 3). Two sources, 2A (Bladen County, N.C.) and 7A (Sabine Parish, LA.) were among the best geographic sources wherever planted. Also, trees from transects 2 and 7 performed best at all plantings in which they were represented.

Despite the lack of significant differences, mean height at plantings 1A, 2B, 3A, and 3B indicate potential physiographic differences. Transects 1 to 4 were divided into Piedmont and Coastal Plain subsamples. For Coastal Plain plantings (2B, 3B), Piedmont sources were as good as Coastal Plain sources. Plantings 6A and 7A had significant physiographic differences but did not conform to the Piedmont-Coastal Plain breakdown of the other plantings.

Further evidence of provenance variation was observed in the mean height of the 14 check-lot families (Figure 2). Check lots of Southern transects tend to do poorer than those of Northern transects at Northern planting areas (plantings 2B, 3A) and vice versa (5A, 6A). Physiographic region differences are also indicated at all plantings. Coastal Plain check lots (transects 1-4) were as good as or better than Piedmont check-lots when planted at Coastal Plain/bottomland plantings (1A, 3A, 5A, 6A, 7A). Piedmont check lots were better than those of the Coastal Plain at planting 2B. Planting 3B was not included because no check trees were measured at age 10.

Table 2.--Results of the analysis of variance for each planting for height and DBH.

Source of variation	Planting 1A - NC Lower Coastal Plain DF	 MS Height	 MS DBH	Planting 2B - SC Piedmont DF	 MS Height	 MS DBH	Planting 3A - SC Coastal Plain DF	 MS Height	 MS DBH
Replications	2			5			5		
Geographic Sources	5	77.46	.805	5	67.41	1.131	4	66.85	1.179**
Transects	2	161.05	.558	2	75.39	.271	2	44.42	1.289**
Physiographic Regions/ Transect	3	23.91	.971	3	68.85	1.596	2	85.84	.978**
Stands/Geographic Source	6	47.61	1.028	5	31.73	.960	5	23.25	.144
Replications X Stands/ Geographic Source	12	22.74*	.435	25	44.37**	.937**	20	13.33**	.223**
Families/Stand/Geographic Source	41	15.65	.433	37	41.64**	1.137**	32	15.63**	.386**
Replications X Families/ Stands/Geographic Source	82	12.31**	.289	185	13.56**	.420**	155	2.33	.078
Within-plot Error	811	6.90	.250	811	8.35	.253	2540	2.24	.072

Source of variation	Planting 3B[a] - SC Piedmont DF	 MS Height	 MS DBH	Planting 5A - AL Lower Coastal Plain DF	 MS Height	 MS DBH	Planting 6A - MS Riverbottom DF	 MS Height	 MS DBH
Replications	5			2			5		
Geographic Sources	5	20.31	.296	5	101.21	1.711	5	91.55	3.411
Transects	2	45.48	.350	2	91.80	2.521	2	70.27	5.832*
Physiographic Regions/ Transect	3	13.16	.429	3	195.55	.803	3	111.49*	2.387
Stands/Geographic Source	5	23.24	.448	5	51.12	.721	5	24.75	.855
Replications X Stands/ Geographic Source	25	38.30**	.739**	12	36.66**	.383*	30	44.74**	.549**
Families/Stand Geographic Source	36	7.40**	.132**	44	8.15	.286	46	12.44*	.391**
Replications X Families/ Stand/Geographic Source	176	2.28*	.058**	83	7.59**	.194**	223	4.41	.157*
Within-Plot Error	2410	1.79	.044	828	3.52	.091	1721	5.12	.132

* - Significant at the .05 level ** - significant at the .01 level

[a] Tenth-year data used for planting 3B.

Table 2. (Continued) -- Results of the analysis of variance.

Source of variation	Planting 7A - LA Branchbottom DF	 MS Height	 MS DBH
Replications	5		
Geographic Sources	5	122.25**	.649
Transects	2	67.24	.466
Physiographic Regions/ Transect	3	159.43**	.773
Stands/Geographic Source	6	6.69	.418
Replications X Stands/ Geographic Source	30	52.95**	.518**
Families/Stand/Geographic Source	48	17.91**	.413**
Replication X Families/ Stands/Geographic Source	239	9.35*	.170
Within-plot error	1770	7.38	.147

* - Significant at the .05 level ** - Significant at the .01 level

Variation among Stands/Geographic Source

No significant variation among stands was detected at any plantings for stand/geographic source variation. Significant stand to stand differences were reported, however, in two earlier papers using data from this study (Johnson and McElwee, 1967; Sprague and Weir, 1973).

Variation among Families/Stand/Geographic Source

The most important source of geographic variation in this study was among families (Table 2). Family differences were significant (.01 level) for height and DBH at plantings 2B, 3A, 3B, 6A, and 7A.

DISCUSSION

The existence of provenance variation across the sampled range of sweetgum is not surprising. The natural range of sweetgum covers a large area (Figure 1) and changes in climate and soils should encourage such variation. Other species with similar ranges (for example, loblolly pine (*Pinus taeda* L.) and sycamore (*Platanus occidentalis* L.)) have similar provenance variation (Wells and Wakeley, 1966; Ferguson *et al*., 1977).

Patterns of geographic source, transect, and physiographic region variation were not consistent at all plantings for all traits. One problem was that only 6 geographic sources, 3 transects, and 2 regions were compared at each planting. With low numbers of degrees of freedom, genetic differences are hard to detect. Other studies that have found geographic source variation in the South tested more sources than were used in this study (Wells and Wakeley, 1966; Wells *et al*., 1979; Land 1981).

Table 3.--Mean height and DBH for each planting by geographic source and transect for fourteenth-year results.

Planting 1A

Geographic Source	Height	DBH
1A	48.9	5.81
1B	48.0	5.63
2A	51.7	5.76
2B	50.3	5.81
7A	52.4	6.20
7B	50.9	5.68

Transect	Height	DBH
1	48.5	5.70
2	51.0	5.80
7	51.7	5.90

Planting 2B

Geographic Source	Height	DBH
1A	47.1	6.04
1B	46.4	5.87
2A	47.9	6.01
2B	48.9	6.17
3A	45.9	5.91
3B	49.2	6.34

Transect	Height	DBH
1	46.8	5.96
2	48.3	6.09
3	47.1	6.07

Planting 3A

Geographic Source	Height	DBH
2A	23.5	2.72
2B	20.3	2.42
3A	21.5	2.48
3B	20.3	2.31
4A	21.6	2.34

Transect	Height	DBH
2	22.6	2.63
3	20.9	2.40
4	21.6	2.34

Planting 3B[a]

Geographic Source	Height	DBH
2A	17.0	1.61
2B	16.4	1.59
3A	14.7	1.33
3B	16.0	1.61
4A	16.2	1.56
4B	16.9	1.62

Transect	Height	DBH
2	16.7	1.60
3	15.5	1.50
4	16.5	1.58

Planting 5A

Geographic Source	Height	DBH
4A	31.9	4.48
4B	37.9	4.79
5A	35.6	4.47
5B	37.7	4.69
6A	38.2	5.16
6B	37.2	4.85

Transect	Height	DBH
4	34.8	4.63
5	36.6	4.57
6	37.7	5.00

Planting 6A

Geographic Source	Height	DBH
5A	47.2	5.18
5B	45.1	5.04
6A	44.6	5.39
6B	44.8	5.17
7A	48.1	5.77
7B	45.1	5.24

Transect	Height	DBH
5	46.2	5.11
6	44.7	5.28
7	46.5	5.48

Planting 7A

Geographic Source	Height	DBH
1A	43.7	4.91
1B	45.6	5.05
6A	44.3	5.03
6B	47.3	5.17
7A	46.9	5.17
7B	45.1	4.98

Transect	Height	DBH
1	44.6	4.98
6	45.8	5.10
7	46.0	5.07

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[a] Planting 3B means are for tenth-year data.

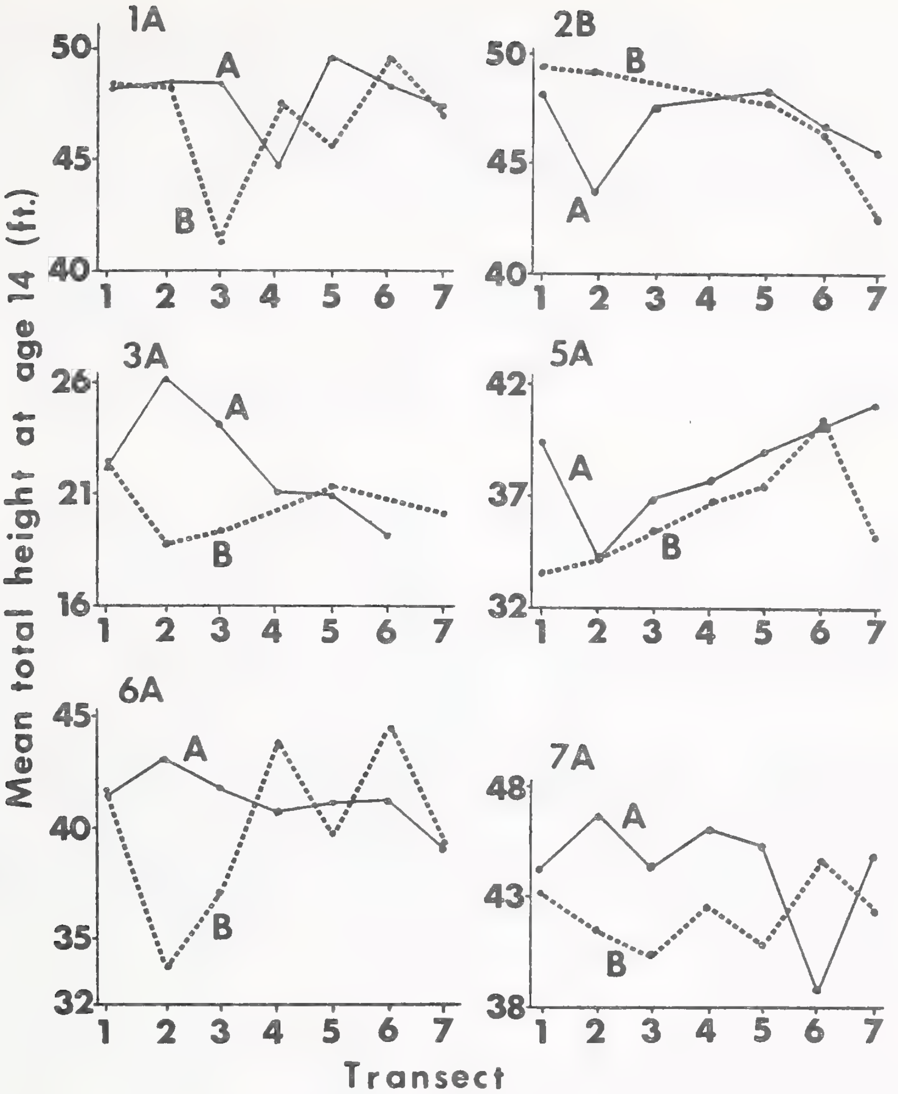

Figure 2.--Height performance of the 14 check lots by transect and physiographic region for the 6 plantings measured at age 14. Transect 1 is the northernmost (North Carolina) and transect 7 is the most southwestern (Louisiana-Texas) (Figure 1.) Plantings 2B and 3A did not include all 14 check lots.

Results do indicate, however, that the choice of geographic seed source can be important in sweetgum. Movement of seed sources long distances can be detrimental, depending upon site and climate. Piedmont sources when planted on Coastal Plain or Bottomland sites did not grow as well as Coastal Plain bottomland sources. Planting of Coastal Plain or Southern sources at colder Piedmont sites can produce poorer growth than local material. A similar pattern of Coastal Plain/Piedmont performance in comparison plantings on respective sites was found for loblolly pine (Wells and Wakeley, 1966).

An exception to the trend of movement of sweetgum sources long distances was planting 1A, located on a fertile North Carolina river flood plain. Southern check lots (Figure 2) and southern geographic sources (Table 3) were taller than local material. Because of the good site and location in the lower Coastal Plain, climatic factors might not have affected growth as they did on the fertile but colder Piedmont site (2B).

Results of two previous studies using data from this study conflict with the fourteenth-year results. Sprague and Weir (1973) found significant stand variation for height at 7 of 10 plantings and significant family height differences at only 3 of 10 plantings for fourth-year results. Johnson and McElwee (1967) reported significant stand and family variation for several wood characteristics from the parent trees of this study.

The different results at age 4 versus 14 come from different statistical analyses. The analysis of variance at age 4 did not include any replication interactions (i.e., replication X geographic source, etc.). For analyses at age 14, these interactions were separated. The replication X geographic source interactions were not significant. However, replication X stand/geographic source interactions were significant in 13 of 14 F-tests (7 plantings X 2 traits) and replication X family/stand/geographic source interactions were significant in 9 of 14 F-tests. The resulting tests showed no significant stand variation. Family differences were significant at 5 of 7 plantings. However, if all replication interactions were combined into a common error term, then stand differences were significant at the two plantings with no family differences in the previous full analysis (1A, 5A). Three studies still had significant family variation (2B, 3A, and 3B) and two others now had no significant family differences (6A, 7A). Combining the significant replication interactions into the error term decreases the power of F-test to detect family variation.

The large replication X stand/geographic source interactions are a result of the study layout. The five families collected from a particular stand are blocked together within a replication. The genetic variation for families within a stand is estimated more accurately than if the five families had been randomly scattered throughout a replication. The two stands per geographic source are not blocked together, however, and are randomized within a replication. Because environmental heterogeneity should be lower within a family block than across a replication, the experimental error for stands should be greater than for families.

Two plantings (1A and 5A) had results which differed from the other 7. Both had only 3 replications; the other 3 had been abandoned because of poor survival and growth. Planting 1A had significant family differences at age 4 and 10 but not at 14. Planting 5A was established on an old field site with much environmental variation across a replication.

STUDY IMPLICATIONS

The large among family variation suggests that mass or family selection should produce good genetic gain. Phenotypic selection in natural hardwood stands is complicated, however, by site variability, relatedness though sprouting, age class variation, and mixture of species. Comparison tree selection for sweetgum is not advisable because neighboring trees are often related by sprouting. Selection of good phenotypes followed by progeny testing is a better method for population improvement of sweetgum.

Geographic origin of seed is important for sweetgum. More sources must be tested to determine the ability to move sources across the South.

Physiographic region differences seem important. Coastal Plain/bottomland sources should be used in their own areas. Piedmont sources should be used in Piedmont plantings.

Tree to tree differences are the most important source of genetic variation in natural populations of sweetgum.

LITERATURE CITED

Barr, A. J., J. H. Goodnight, J. P. Sall, W. H. Blair, and D. M. Chilko. 1979. SAS User's Guide: 1979 Edition. SAS Institute, Raleigh, N. C. 494 p.

Ferguson, R. B. and D. T. Cooper. 1977. Sweetgum variation changes with time. Proc. 14th Southern For. Tree Imp. Conf. p. 194-200.

Ferguson, R. B., S. B. Land, Jr., and D. T. Cooper. 1977. Inheritance of growth and crown characters in American sycamore. Silvae Gen. 26:180-182.

Johnson, J. W. and R. L. McElwee. 1967. Geographic variation in specific gravity and three fiber characteristics of sweetgum. Proc. 9th Southern For. Tree Imp. Conf. p. 50-55.

Land, Jr., S. B. 1981. Genetic variation, heritabilities, and selection strategies for early growth of sycamore in the Gulf South. Proc. 16th Southern For. Tree Imp. Conf. p. 123-135.

Satterthwaite, F. E. 1946. An approximate distribution of estimates of variance components. Biom. Bull. 2:110-114.

Sprague, J. and R. J. Weir. 1973. Geographic variation of sweetgum. Proc. 12th Southern For. Tree Imp. Conf. p. 169-180.

Webb, C. D. 1964. Natural variation in specific gravity, fiber length, and interlocked grain of sweetgum (Liquidambar styraciflua L.) in the South Atlantic States. Unpublished PhD thesis, North Carolina State Univ. 138 p.

Wells, O. O., G. L. Switzer, and W. L. Nance. 1979. Genetic variation in Mississippi sweetgum. Proc. 15th Southern For. Tree Imp. Conf. p. 22-32.

Wells, O. O. and P. C. Wakeley. 1966. Geographic variation in survival, growth, and fusiform rust infection of planted loblolly pine. For. Sci. Monog. 11. 40 p.

VARIATION, HERITABILITY AND GAIN IN CONIFERS

FIFTH YEAR PERFORMANCE OF WIDE RANGING LOBLOLLY PINE PROVENANCES

John A. Pait, III and Lee Draper, Jr.[1]

Abstract.-- Five provenances of loblolly pine were planted at six locations in north Florida and south Georgia. After five growing seasons, the East Texas source had the lowest fusiform rust infection in most tests and exhibited fair growth rate. The Livingston Parish source incurred surprisingly high rust infection, but generally ranked well in growth. Marion County, Florida and north Florida Seed Orchard stock grew well, but sustained high rust infection. The Eastern Shore of Maryland source was intermediate to East Texas and Livingston Parish in rust infection, but ranked lowest in growth in most tests. Livingston Parish and local sources are not recommended for planting in high rust hazard areas.

Additional keywords: *Pinus taeda*, *Cronartium quercuum* f. sp. *fusiforme* resistance, geographic variation.

The use of loblolly pine (*Pinus taeda* L.) in Container Corporation of America's regeneration efforts has steadily increased in the past 20 years. In 1982 and 1983 more than half of Container's reforestation was devoted to this species. Early decisions concerning the best loblolly seed sources for Company lands were made based on the Southwide Pine Seed Source (Wells, 1969) and in-house provenance tests (Draper, 1975). These studies indicated that the best provenances for use in north Florida and south Georgia were Marion County, FL, Livingston Parish, LA, and East Texas. To best use these sources on Company lands, a partial combination of the Southwide Study and our in-house tests was required. The result was the installation of several tests across CCA lands in 1976 and 1977. Fifth year measurements suggest continued use of all three aforementioned provenances with changes in geographic allocation that should minimize fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*) infection and maximize growth rate.

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The authors express their sincere thanks to Brunswick Pulp and Land Company for the establishment and measurement of the Liberty County, Georgia test. We also thank Patricia Layton, University of Florida, for her assistance in data analysis.

METHODS

Seed Sources and Test Establishment

The objective of the study was to evaluate East Texas, Livingston Parish, Marion County, FL, northeast Florida, and Eastern Shore of Maryland sources for reforestation on a variety of loblolly pine sites in north Florida and south Georgia.

East Texas seed was provided by Southwestern Lumber Corporation. Seed from the eastern third of Livingston Parish, LA was provided by the United States Forest Service (courtesy of O. O. Wells). Seed from the eastern half of Marion County, FL was collected following a logging operation. Seed representing northeast Florida came from an unrogued, first generation seed orchard composed of northeast Florida and southeast Georgia selections. Seed from the Eastern Shore of Maryland was provided by the Chesapeake Corporation. These five sources were sown in Container's nursery near Archer, FL in the spring of 1975.

During the dormant season of 1975-76 seedlings of each of the five sources were lifted and dibble planted in Madison, Marion, and Nassau Counties, Florida and Randolph, Telfair, and Liberty Counties, Georgia (Figure 1). The test design consisted of a 49 tree (seven rows X seven trees per row; spacing of 6 feet X 10 feet) rectangular plot of each source randomly as- signed to each of four replications (196 trees per source per test). Poor initial survival due to drought necessitated re- peating the Marion County, FL and Randolph County, GA tests in the 1977 planting season. By accident, seed orchard slash pine was planted in the Marion County, FL and Randolph County, GA tests instead of the north Florida - south Georgia seed orchard (SO) source. Their performance will not be discussed.

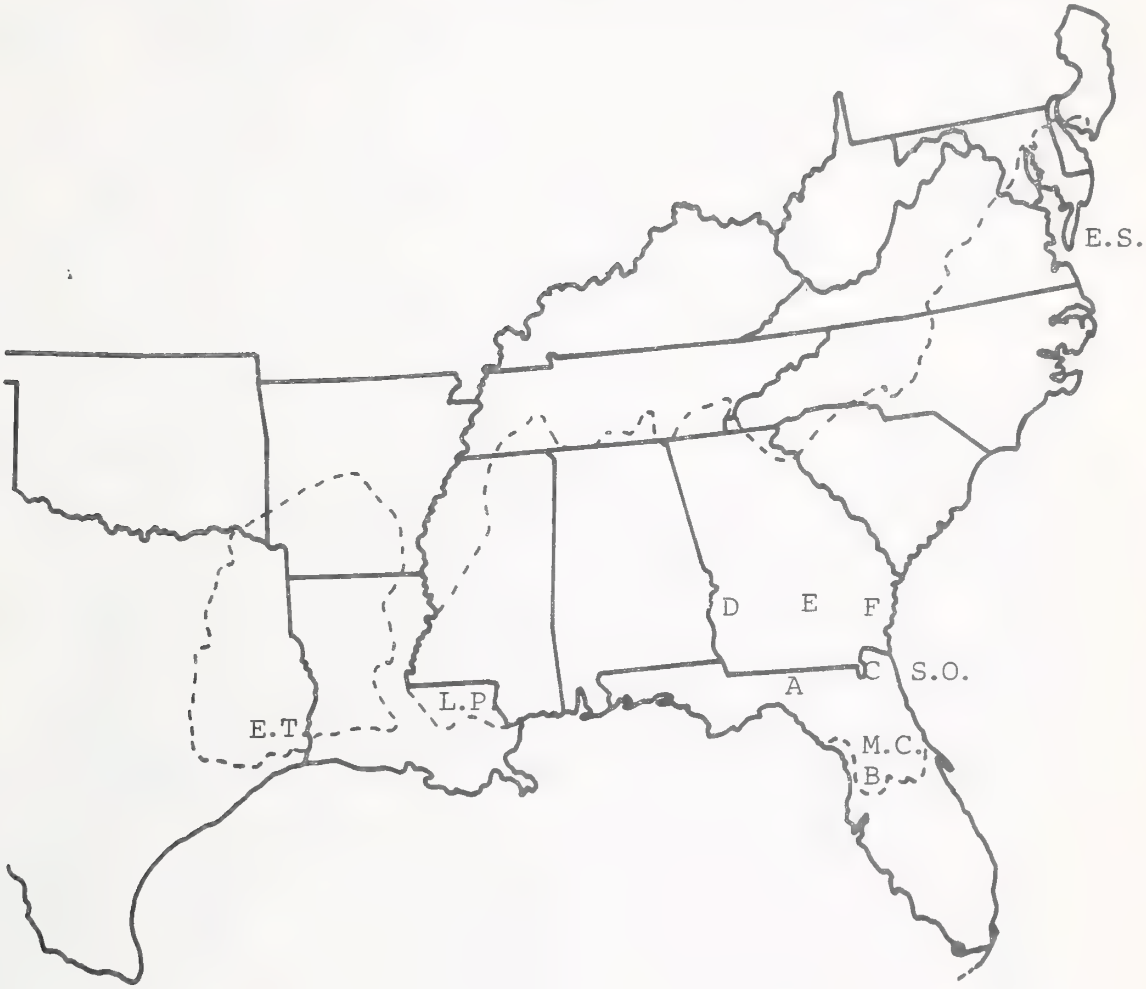
Measurements and Analyses

Fusiform rust infection, survival, total height, and diameter at breast height were tallied in five of the six tests at age five. Only total height and rust infection were measured in the Liberty County, GA test. No distinction was made between stem and limb rust infection in any of the tests.

Since source-performance at each location was of primary interest, analyses of variance were conducted for each parameter within each test. Source means within each test were separated using Duncan's multiple range test at the 0.05 level of probability.

Figure 1:

CONTAINER CORPORATION OF AMERICA LOBLOLLY PINE PROVENANCE TESTS



Seed Sources:

E.T. - East Texas
L.P. - Livingston Parish
M.C. - Marion County
S.O. - North Florida Seed Orchard
E.S. - Eastern Shore Of Maryland

Plantations:

A - Madison County, FL
B - Marion County, FL
C - Nassau County, FL
D - Randolph County, GA
E - Telfair County, GA
F - Liberty County, GA

- - - - : Dashed line delineates natural range of loblolly pine.

RESULTS AND DISCUSSION

Fusiform Rust

Average fifth year fusiform rust infection ranged from 6.0% (Nassau County, FL) to 44.9% (Madison County, FL). Significant source differences were present in all but the lightly infected Nassau County, FL test (Figure 2a.). The East Texas incurred the lowest infection rate in all tests except Nassau County, FL. The Eastern Shore of Maryland and Livingston Parish sources sustained relatively low and similar infection rates except in Madison County, FL. In this test, the Livingston Parish source was the most highly infected of all; 73.5% versus 14.3% and 24.5% for East Texas and Eastern Shore of Maryland sources, respectively. The Seed Orchard and Marion County, FL sources sustained the highest levels of infection in the Telfair and Liberty Counties, GA tests. The Seed Orchard source was highly infected relative to other sources in the Liberty County, GA test; 65.4% versus 39.1%, 30.8%, 28.2%, and 17.8% for the Marion County, Eastern Shore of Maryland, Livingston Parish and East Texas sources respectively. The Marion County source was severely infected in the Marion County, FL test; 60.1% versus 16.7%, 16.3% and 7.6% for the Eastern Shore of Maryland, Livingston Parish, and East Texas sources respectively.

It is unclear why the Livingston Parish source was so highly infected relative to the other resistant sources in the Madison County, FL test. One explanation is the possibility of interaction between its source and local sources of rust spores. Considerable pathogenic diversity in fusiform rust has been reported to exist among diverse geographic areas, among galls within the same area, and within a single gall (Schmidt et al, 1981). Variation in rust resistance within Livingston Parish may have contributed to the source's high rates of infection. If so, more specific information on seed origin will be required for use of this source in high rust areas.

Use of local sources in high hazard rust areas is not recommended. Pathogenic adaptation to local sources has been demonstrated artificially (Powers et al, 1977 and Powers and Matthews, 1980) and recently reported with respect to the Southwide Pine Seed Source Study (Wells, 1983). The 60.1% level of infection in the Marion County source and light infections in other sources planted in the Marion County, FL test (Figure 2a.) further corroborate such findings.

Survival

Average fifth year survival ranged from 65.4% (Telfair County, GA) to 97.3% (Nassau County, FL). Significant source

Figure 2a:

Fifth year fusiform rust infection by seed source and test plantation.[a]

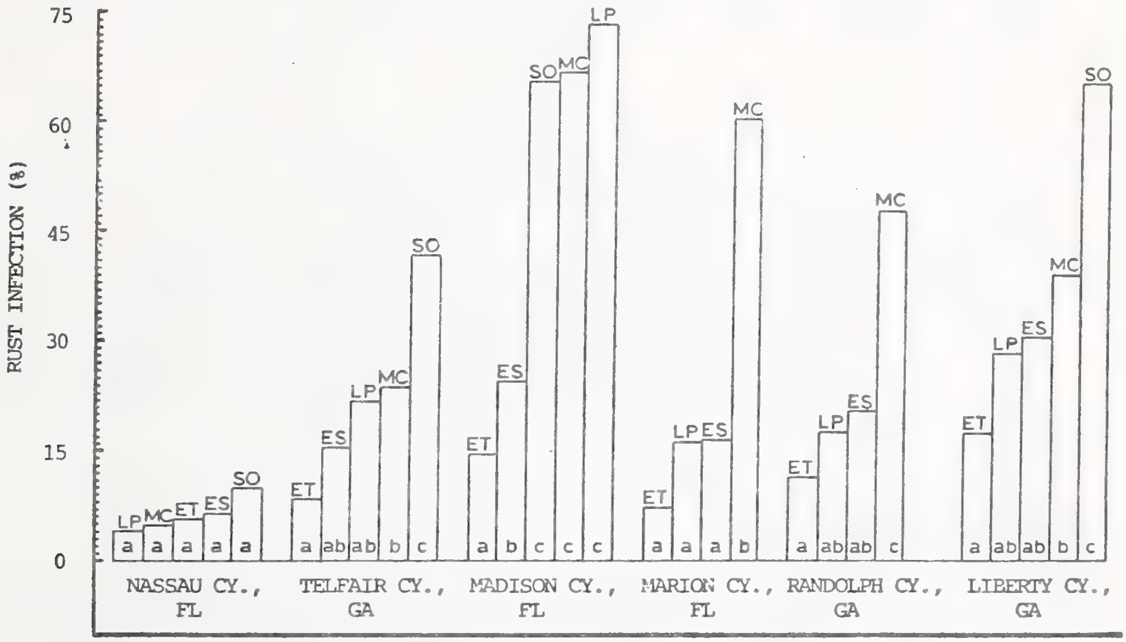
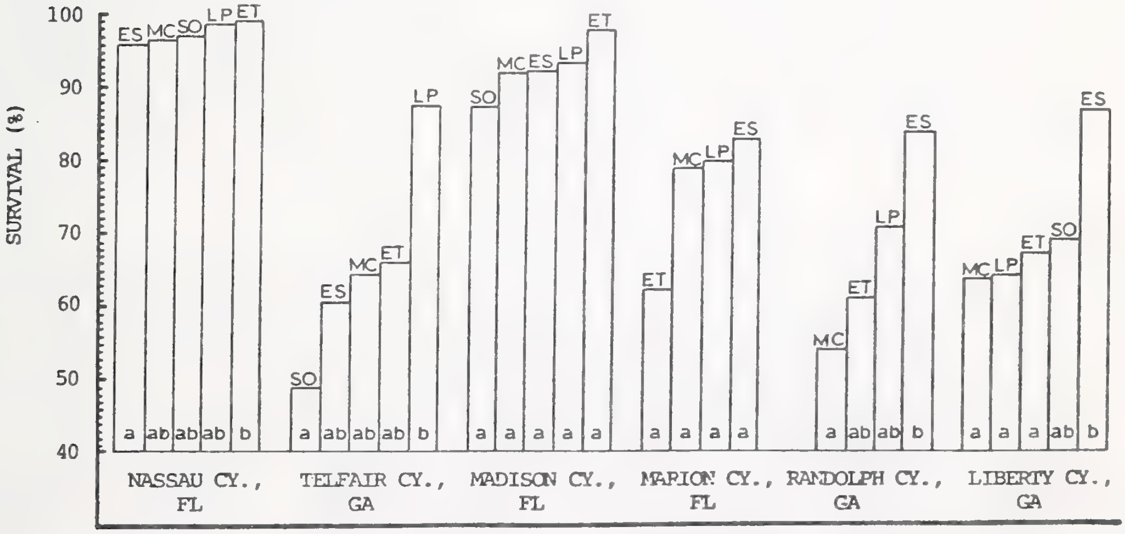


Figure 2b:

Fifth year survival rates by seed sources and test plantation.[a]



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[a] Bar heights (source means within test) enclosing similar letters are not significantly different according to Duncan's multiple range test; 0.05 level of probability.

differences were present in all but the Madison County and Marion County, FL tests (Figure 2b.). Generally these differences were only significant between the highest and lowest survival rates. The poor survival of most sources in the Telfair and Randolph Counties, GA tests was due to drought following planting. Feral pigs caused considerable damage in some plots of the Liberty County, GA test. This may explain the fairly low survival rates of all sources except Eastern Shore of Maryland sources (86.2%).

Height

Average fifth year heights ranged from 8.0 feet (Nassau County, FL) to 13.5 feet (Madison County, FL). Significant source differences were present in all but the Liberty County, GA test (Figure 3a.). The Livingston Parish source was tallest in three of the six tests but never significantly different from the East Texas source. The Marion County source was significantly tallest in the Marion County, FL test. The Eastern Shore of Maryland source ranked last in five of the six tests; it was significantly shortest in three of the five.

Diameter

Average fifth year diameters at breast height ranged from 1.3 inches (Nassau County, FL) to 2.7 inches (Madison County, FL). Significant source differences were present in all but the Nassau County, FL test (Figure 3b.) and Liberty County, GA test (not measured). The Eastern Shore of Maryland source was significantly smallest in the Madison County and Marion County, FL tests in which it was also the shortest. The Livingston Parish source in Madison County, FL was the largest of all sources in all tests (3.2 inches). The Marion County source was significantly the largest of all sources in the Marion County, FL test.

CONCLUSION

Although the data pertain to young tests several trends are clear. The best of the five sources for planting in high hazard rust areas appear to be that from East Texas. This source exhibited surprising stability in rust resistance even in the Madison County, FL test where the Livingston Parish source incurred a 73.5% infection and East Texas only a 14.3% infection. Though the Eastern Shore of Maryland source is fairly rust resistant, its height and diameter performance indicate poor adaptation to north Florida or south Georgia.

Based on current findings, the Livingston Parish source is not recommended for high hazard rust areas. Where fusiform rust is not a major consideration, local, Livingston Parish or Marion County sources are recommended for planting within normally recognized latitudinal limits.

Figure 3a:

Fifth year total heights by seed source and test plantation. [a]

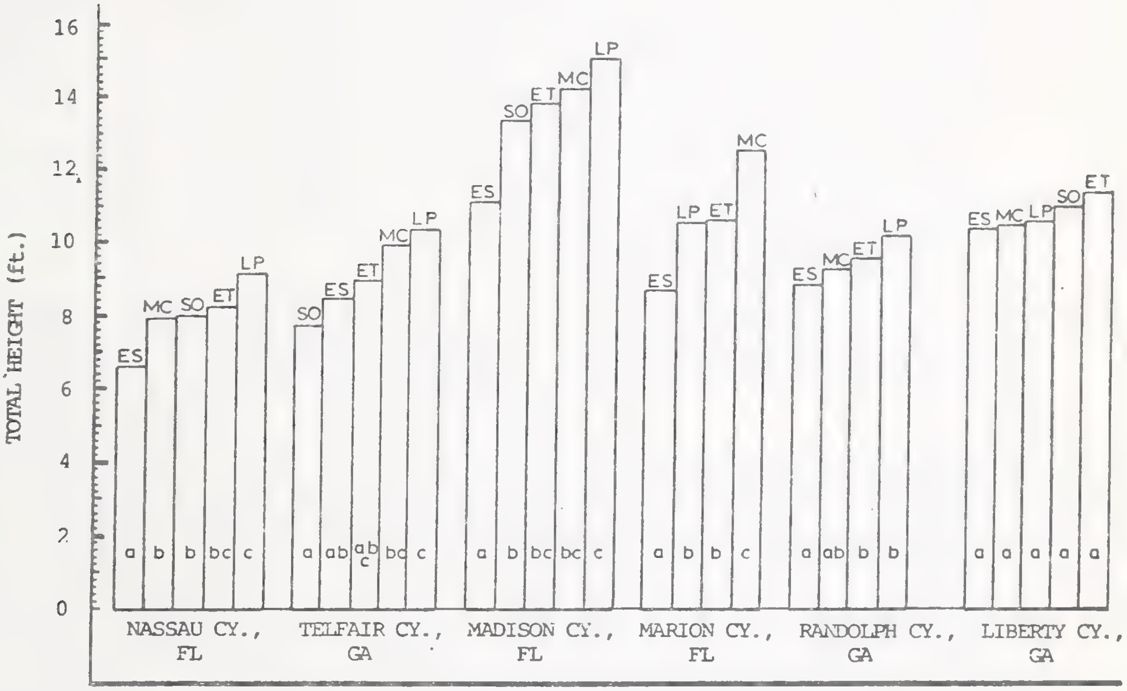
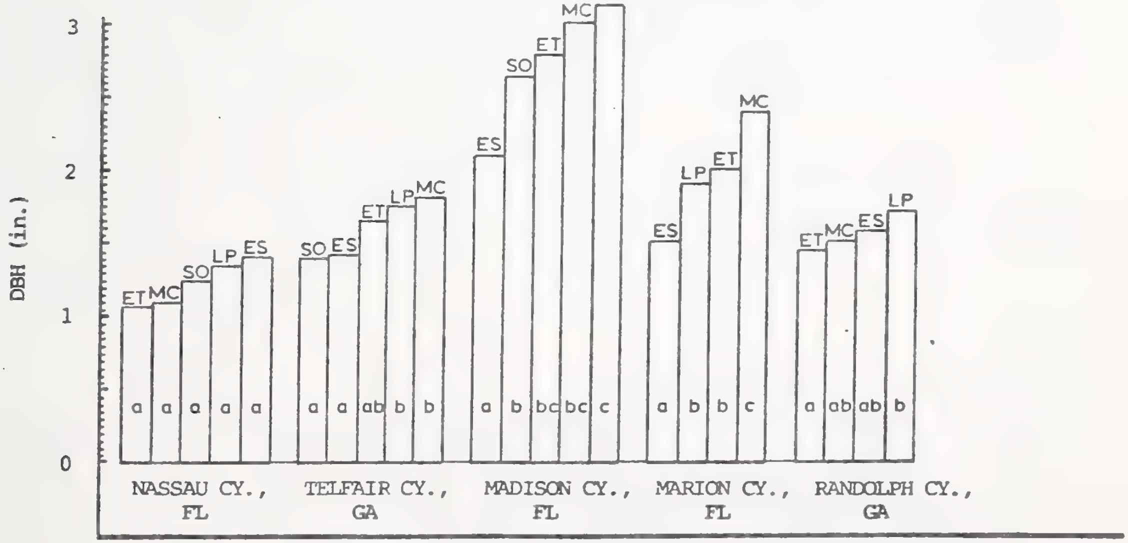


Figure 3b:

Fifth year dbh by seed source and test plantation. [a]



[a] Bar heights (source means within test) enclosing similar letters are not significantly different according to Duncan's multiple range test; 0.05 level of probability.

LITERATURE CITED

Draper, L., Jr. 1975. Provenance study of five geographic sources of loblolly pine. Pages 83-88 in : Proc. 13th South. For. Tree Improv. Conf., 10-11 June 1975, Raleigh, N.C. Published by South. For. Tree Improv. Comm. 262 pp.

Powers, H. R., Jr., F. R. Matthews, and L. D. Dwinell. 1977. Evaluation of pathogenic variability of Cronartium fusiforme on loblolly pine in the Southern USA. Phytopathology 67 : 1403-1407.

Powers, J. R., Jr., and F. R. Mathews. 1980. Comparison of six geographic sources of loblolly pine for fusiform rust resistance. Phytopathology 70 : 1141-1143.

Schmidt, R. A., H. R. Powers, Jr., and G. A. Snow. 1981. Application of genetic disease resistance for the control of fusiform rust in intensively managed southern pine. Phytopathology 71 : 993-997.

Wells, O. O., 1969. Results of the southwide pine seed source study through 1968-1969. Pages 117-129 in : Proc. 10th South. For. Tree Improv. Conf.

______________ 1983. Southwide pine seed source study -- loblolly pine at 25 years. South. Jour. App. For. 7:2: 63-70.

THREE INCREMENTS OF GAIN FROM THREE STAGES OF SELECTION IN SLASH AND LONGLEAF PINES AND HERITABILITIES AT AGE 21 YEARS

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Abstract.--Three tandem stages of selection--individual, family, and within-family--performed in slash and longleaf pines produced good increments of gain in most of seven traits in most stages. Gains in d.b.h. and volume per tree were low or negative for the first two increments, but selection within families was very effective in producing gains in these two traits. Selection among families was primarily for rust resistance and produced large gains in that trait. Heritabilities were moderately strong to strong for most traits. Selection among families for a critically important trait needs to be followed by within-family selection to recoup losses and secure desired gains in other traits

Additional keywords: Progeny testing, mass selection, family selection, within-family selection, selection differential, disease resistance, *Pinus elliottii* var. *elliottii*, *P. palustris*, *Cronartium quercuum* f. sp. *fusiforme*.

Breeding plans for forest trees can vary from very simple mass selection to very elaborate combinations of selection and progeny testing. Generally, the more elaborate the plan, the greater the genetic gain per generation and the greater the total cost. The choice of plan depends upon the objectives and resources of the particular organization involved.

Breeding plans commonly used for forest trees include one or more of the following three stages: phenotypic selection from a mass population, progeny testing and selection among families, and selection of individuals within selected families. Each stage has its own set of costs and produces its own increment of gain. So there is considerable interest in what happens in each stage and how best to allocate resources among them (Cotterill and James, 1981; Namkoong and others, 1966).

Several progeny test plantations established in central Georgia by the Southeastern Forest Experiment Station are now near pulpwood rotation age and provide an excellent opportunity to evaluate gains from the three stages of selection in slash (*Pinus elliottii* Engelm. var. *elliottii*) and longleaf (*P. palustris* Mill.) pines.

METHODS

Trees used to begin this study were slash pines selected from plantations of unknown provenance in Jones and Dooly counties and longleaf pines selected from natural stands in Bleckley and Dooly counties, Georgia (selection stage one). This first stage of selection was done without a formal selection index. Instead, choices were made by measuring tree size and subjectively evaluating several form traits. Almost all the trees selected were free of fusiform rust (Cronartium quercuum (Berk.) Miyabe ex. Shirai f. sp. fusiforme) cankers.

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Several progeny tests were established, but for this paper data from only three will be used, two of slash and one of longleaf pine. Each plantation was numbered. Numbers 38 and 50 are slash pine and number 49 is longleaf pine. Plantation 38 contained wind-pollinated progenies from 27 trees and plantation 50 contained wind-pollinated progenies from seven trees plus 11 full-sib progenies from single crosses among 17 trees. Longleaf plantation 49 contained wind-pollinated progenies from seven trees and six full-sib progenies from crosses among eight trees.

Traits evaluated in the progeny tests at age 21 years were survival, height, d.b.h., tree volume, rust-free percentage, stem crook, and volume per hectare. Heritabilities and phenotypic standard deviations on both a family and an individual basis were calculated from the data from wind-pollinated (half-sib) progenies.

Selection among and within families (stages two and three) was performed in the progeny tests. The trait used for selection among families was rust-free percentage. For selection within families, only rust-free trees with good size and form traits were selected. Again, no formal selection index was used. Only one tree per selected family was chosen in plantation 38. In each of the other two plantations the best tree on each plot of each selected family was chosen in all but two plots which had no suitable trees.

For each trait, actual gain produced by each stage of selection was calculated. For stage one, gain was the mean of all the families compared to the check. For stage two, it was the mean of the selected families compared to the mean of all the families and for stage three, it was the mean of the selected trees compared to the mean of the selected families. These gains were calculated for each plantation. Each increment of gain was also expressed as a percentage of its base.

To estimate the gain in performance expected to be inherited by progenies from the second-generation selections, each increment of gain was multiplied by its applicable heritability, the increments summed, and the sums compared to the check mean for each trait.

RESULTS

The means for all the families, selected families, trees selected within families, and checks are listed for each plantation in table 1. Gains and other data are shown in tables 2 through 8.

Stage 1, Mass Selection

Gains over checks from mass selection were greatest for survival, percentage rust free, and volume per hectare, three traits which are positively correlated (tables 2 and 3). Moderate gain was made in stem straightness. Gains in height and d.b.h. were low. In fact, there was a loss in mean d.b.h. for the longleaf, associated most likely with the good gain in survival percentage. Survival and d.b.h. were strongly inversely correlated in the longleaf pine.

Table 1.--Data means at age 21 for two slash and one longleaf pine progeny tests

Group	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Slash pine plantation 38				
All families (27)	32.8	18.4	26.7	30.3	3.30	0.372	128.9
Best 7 families[a/]	52.8	19.1	25.9	65.9	2.97	.359	200.1
Selected trees (7)		20.9	31.2		1.29	.606	
Check	25.4	17.6	26.9	20.5	3.49	.362	91.9
			Slash pine plantation 50				
All families (18)	48.9	17.8	22.3	21.9	3.15	.247	127.0
Best 4 families[a/]	62.7	18.0	21.9	51.5	2.72	.241	158.3
Selected trees (14)		20.0	25.7		1.93	.386	
Check	39.1	17.4	21.6	12.6	3.69	.231	93.2
			Longleaf pine plantation 49				
All families (13)	46.9	17.7	23.3	25.9	2.90	.270	129.1
Best 4 families[a/]	45.7	18.0	23.7	42.5	2.84	.287	131.7
Selected trees (14)		19.4	26.2		2.14	.384	
Check	32.7	17.3	24.6	22.6	3.33	.295	98.5

[a/] Best in rust resistance.

Selection differentials were less than one standard deviation for all traits except height in plantation 38; stem crook and volume per hectare in plantation 50; and survival, stem crook, and volume per hectare in plantation 49 (table 4). Family heritabilities were moderate to high for most traits, but height in plantation 50 and stem crook and volume per hectare in plantation 49 had zero heritabilities (table 6).

Stage 2, Selection Among Families

Since selection among families was based primarily on rust resistance, by far the greatest percentage gain from this stage was in the rust free percentage (table 3). Good gains also were realized in survival and volume per hectare for slash pine plantations 38 and 50, but not for longleaf pine plantation 49. In all three plantations, this stage of selection yielded little or no gain in height and d.b.h. Again, selection differentials were low except for the rust-free and associated traits (table 4). However, a high selection differential for rust-free percentage was not accompanied by high selection differentials for survival and volume per hectare in longleaf pine. Heritabilities and phenotypic standard deviations were the same for this stage as for stage one (tables 5 and 6).

Table 2--Actual gains at age 21 from three stages of selection

Selection Stage	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Mass[a]	7.4	0.8	-0.2	9.8	0.19	0.010	37.0
Family[b]	20.0	.6	- .8	35.6	.13	- .013	73.2
Within family[c]		1.8	5.3		1.88	.247	137.7[d]
			Plantation 50				
Mass	9.8	.4	.7	9.3	.54	.016	33.8
Family	13.8	.2	- .4	29.6	.43	-.006	31.3
Within family		2.0	3.8		.79	.145	95.2[d]
			Plantation 49				
Mass	14.2	.4	-1.3	3.3	.43	-.025	30.6
Family	-1.2	.3	.4	16.6	.06	.017	2.6
Within family		1.4	2.5		.70	.097	44.5[d]

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a/ Means of all the families compared to the means of the check.
b/ Means of selected families compared to the means of all the families
c/ Means of selected trees compared to the means of selected families.
d/ Gains if all trees in selected families were as large as selected trees.

Table 3--Actual gains at age 21 from three stages of selection, expressed as percentage of the base

Selection Stage	Trait Survival	 Height	 D.b.h.	 Rust free	 Stem crook	 Volume/ tree	 Volume/ ha
	Percent						
				Plantation 38			
Mass[a]	29.1	4.6	-0.01	47.8	5.4	2.8	40.3
Family[a]	61.0	3.5	-0.03	117.4	4.0	- .03	56.8
Within family[a]		9.6	20.3		59.3	68.8	68.8[a]
				Plantation 50			
Mass	25.1	2.3	3.2	73.8	14.6	6.9	36.3
Family	28.2	1.1	-1.8	135.1	13.6	-2.4	24.6
Within family		11.1	17.3		29.0	60.2	60.2[a]
				Plantation 49			
Mass	43.4	2.3	-5.3	14.6	12.9	-8.5	31.1
Family	-2.6	1.2	1.7	64.1	2.1	6.3	2.0
Within family		7.8	10.5		24.6	33.8	33.8[a]

[a] See footnotes to table 2.

Table 4--Selection differentials used at three stages of selection

Selection Stage	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume ha/
			Plantation 38				
Mass[a]	.47	1.08	-0.12	0.40	0.49	0.19	0.62
Family[a]	1.27	.87	- .46	1.45	.33	- .24	1.24
Within family[a]		.88	1.00		1.55	1.24	2.33[a]
			Plantation 50				
Mass	.71	.53	.49	.70	1.93	.43	1.08
Family	1.01	.27	- .28	2.22	.22	- .16	1.00
Within family		1.23	.94		.81	1.20	3.04[a]
			Plantation 49				
Mass	1.09	.78	- .98	.26	1.54	.64	1.61
Family	- .09	.59	.30	1.29	.21	.44	.14
Within family		.96	.66		.83	1.07	2.34[a]

[a] See footnotes to table 2.

Table 5--Phenotypic standard deviations among and within families for the traits at age 21 years

Basis	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Family	15.7	0.75	1.73	24.5	0.39	0.053	59.2
Within family		2.08	5.28		1.21	.199	
			Plantation 50				
Family	13.7	.75	1.42	13.3	.28	.037	31.3
Within family		1.62	4.04		.97	.121	
			Plantation 49				
Family	13.0	.51	1.33	12.9	.28	.039	19.0
Within family		1.46	3.80		.84	.091	

Table 6--Heritabilities at age 21 years, on a family mean and an individual tree basis

Basis	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Family	0.86	0.19	0.55	0.82	0.34	0.45	0.89
Within family		.25	.24		.13	.20	
			Plantation 50				
Family	.84	0	.61	.88	.77	.43	.78
Within family		0	.20		.28	.19	
			Plantation 49				
Family	.70	.43	.83	.80	0	.91	0
Within family		.36	.33		0	.57	

Stage 3, Selection Within Families

Selection within families produced good gains in the four individual-tree traits--height, d.b.h., stem crook, and volume per tree. Selection differentials generally were higher and heritabilities lower than for the same traits in stages one and two.

Total Gains Over Checks

Among the seven traits, total gain percentages over checks were the greatest for the rust free trait (tables 7 and 8). Good total gains were made in all other traits as well, particularly in survival and volume per hectare. Gains were higher in slash than in longleaf pine. After gains were weighted with heritabilities, the data showed that plantations from seed produced by the trees selected from these families are expected to be about 50 percent rust free for slash pine and about 40 percent rust free for longleaf pine. These two figures compare with 20 percent or less rust free for the checks (table 1), which are assumed to be representative of the general population. The only traits not expected to show some gain were height for progenies of trees selected in plantation 50 and stem crook for progenies of trees selected in plantation 49--heritabilities in these instances were zero.

Table 7--Gains x heritabilities at age 21 years for three stages of selection[a]

Selection Stage	Trait Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Mass[b]	6.4	0.15	-0.11	8.0	0.06	.004	32.9
Family[b]	17.2	.12	- .44	29.2	.04	- .006	65.1
Within family[b]		.46	1.26		.24	.049	27.5[b]
			Plantation 50				
Mass	8.2	0	0.43	8.2	.42	.007	26.4
Family	11.6	0	- .24	26.0	.33	-.003	24.4
Within family		0	.76		.22	.027	18.1[b]
			Plantation 49				
Mass	9.9	.17	-1.08	2.6	0	-.023	0
Family	- .8	.09	.33	13.3	0	.015	0
Within family		.50	.82		0	.055	25.4[b]

[a] These are increments of gain expected to be expressed in plantations established from bulk seedlings from the second-generation selections

[b] See footnotes to table 2.

DISCUSSION

Cost per unit gain is lowest in stage one (Namkoong, 1970), but tree breeders may not want to choose among the three stages of selection done here. Rather they may want to know whether the gains from each stage would pay the costs involved and still be profitable in a forestry operation. The gains reported here were substantial in all stages for slash pine when viewed as the end product, volume per unit area. Even the third stage should increase volume per unit area. The expected gain is: gain in volume per tree x its heritability x the number of trees per unit area. That was the only source of expected gain in volume per hectare in the longleaf pine (table 7).

Gain in some traits may require more than the simplest stage of selection. Until better technology is developed, proper evaluation of selections for rust resistance requires at least some form of progeny testing. By far the greatest gains in that trait were made in selection among families in these plantations (table 7).

Table 8.--Total heritable gains over checks at age 21 years, amounts and percentages

	Trait						
	Survival	Height	D.b.h.	Rust free	Stem crook	Volume/ tree	Volume/ ha
	Percent	m	cm	Percent		m^3	m^3
			Plantation 38				
Amount	23.6	0.7	0.7	37.2	.35	.048	125.6
Percent	92.8	4.2	2.6	181.6	10.0	13.3	136.7
			Plantation 50				
Amount	19.8	0	.9	34.2	.97	.035	68.9
Percent	50.6	0	4.4	271.7	26.2	15.1	73.9
			Plantation 49				
Amount	9.1	.8	.5	15.9	0	.048	25.4
Family	27.8	4.6	2.0	70.4	0	16.3	25.8

If only simple mass selection were done, good gains in a combination of traits in one generation would require use of an elaborate and accurate selection index. Such an index may not be effective for some critical traits such as rust resistance. With the use of two or more stages there is flexibility in concentrating on different traits in the most effective stages. One very beneficial effect of using the third stage in this study was the recovery of some losses in height and d.b.h. which occurred when families were selected primarily on the rust resistance trait.

Gains from the first two stages of selection would be realized in a rogued first-generation clonal seed orchard. Gains from all three stages would be realized in a seedling seed orchard, a good reason to include seedling seed orchards as part of a tree improvement program.

Literature Cited

Cotterill, P.P., and James, J.W. 1981. Optimizing two-stage independent culling selection in tree and animal breeding. Theor. Appl. Genet. 59: 67-72.

Namkoong, Gene. 1970. Optimum allocation of selection intensity in two stages of truncation selection. Biometrics 26(3): 465-476.

Namkoong, Gene; Snyder, E.B., and Stonecypher, R.W. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silvae Genet. 15: 76-84.

RELATION BETWEEN HEIGHT GROWTH AND FUSIFORM RUST INFECTION IN SLASH PINE [1]

A. E. Squillace, P. A. Layton, and R. E. Goddard [2]

Abstract.--Data from four open-pollinated slash pine progeny tests were analyzed to study relationships between growth rate and several measures of fusiform rust infection. Genetic correlations, estimated from half-sib variances and covariances, were variable among tests but usually negative, suggesting that selection for rapid growth will not cause a loss in rust resistance and may increase it slightly. Environmental correlations were positive at young ages, when number of cankers per tree or percent infected trees was used as a measure of infection. Practical implications of the results are discussed.

Additional keywords: *Pinus elliottii* Engelm., forest genetics, forest tree improvement.

The relationship between growth rate and fusiform rust infection in slash (*Pinus elliottii* Engelm.) and loblolly pines (*P. taeda* L.) is unclear. A number of reports (cited by Rowan and Steinbeck 1977) have shown that site factors and cultural practices (such as cultivation and fertilization) which increase growth rates also tend to increase rust incidence. On the other hand, several authors (cited by Dorman 1976, p. 193 and 257) reported little or no relationship between growth rates of families or individual trees and infection in progeny tests.

To our knowledge none of the past studies have attempted to determine the nature of the relationship from a genetic standpoint. The overall association between two traits in members of a population is called the "phenotypic correlation". It is not particularly revealing, because it is a composite of the "genetic correlation" and the "environmental correlation". The genetic correlation is a measure of the degree to which the two traits are affected by the same gene or genes. The environmental correlation is a measure of the degree to which the two traits are affected by similar differences in environmental conditions. (For more precise definitions and discussion of these terms see Falconer 1960, p. 312). Each of these correlations may be positive or negative. If the genetic and environmental correlations differ in sign, the phenotypic correlation may be 0 or close to it.

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[1] This study was sponsored jointly by the Georgia Forestry Commission, Southeastern Forest Experiment Station (USDA Forest Service), and University of Florida.

[2] Adjunct Professor, University of Florida and Volunteer, USDA Forest Service; Graduate Assistant, University of Florida; and Professor, University of Florida. The authors are grateful to Scott Paper Co. for providing progeny test data used in the study and to Dr. Charles J. Wilcox for guidance with statistical analyses.

The genetic correlation is especially important to tree breeders. If, for example, the genetic correlation between growth rate and rust infection is strongly positive, selection for rapid growth alone would result in increased infection, and simultaneous selection for superiority in these traits would be difficult. Appreciable environmental correlations also are important to the breeder because they may suggest the need for covariance adjustments when assessing breeding values of selections for each trait. In this report, we estimate the three types of correlations between growth rate and fusiform rust infection in slash pine.

METHODS

In this study we utilized data from four open-pollinated progeny test plantations (Table 1). They involved a total of 52 different families and 3 check lots. The parents of the families had been selected mainly for rapid growth and desirable tree form. All plantations contained 10-tree single-family row plots, randomly assigned within each of 10 replications. Some of the families were planted in 2 or more of the tests and all check lots were included in all tests. At 3 or 4 years of age, tree heights were measured and stem and limb galls were counted on each tree. At 10 years, heights were again measured, and presence or absence of galls was noted.

Table 1.--Details of the slash pine plantations studied. [a]

Test number	Year established	Ages when measured (years)	Number of families [b]
7	1967	4 and 10	16
8	1967	4 and 10	21
9	1967	3 and 10	21
10	1968	3	41

[a] All plantations were established by Scott Paper Co., in Escambia Co., AL. All families were established from open pollinated seed collected in a seed orchard at Greene Co., MS.

[b] Three check lots were also included in each test. Two were from natural stands and one was from a commercial source.

Components of variance and covariance were analyzed (Falconer 1960, p. 312; Helwig and Council 1979) to estimate genetic, environmental, and phenotypic correlations between tree height and 1) number of limb galls per tree, 2) number of stem galls per tree, 3) number of limb plus stem galls per tree and, 4) percent of trees infected in each plot. Analyses involving limb and stem galls were on an individual-tree basis, while analyses of percent infection were on a plot mean basis. Percentages of trees infected at 3 or 4 years and at 10 years included trees that had died from infection.

RESULTS

Genetic correlations between tree height and various measures of infection varied among tests but were usually negative at both young (3 or 4 years) and older (10 years) ages (Table 2). Negative correlations suggest that trees with inherently rapid growth tend to be more resistant to fusiform rust than inherently slow growers (or similarly, that resistant trees tend to grow more rapidly). The variation among tests may have been partly due to differences in the overall infection among tests. Tests 8 and 9 had the lowest overall infection percentages (Table 3) and showed the strongest negative correlations. Tests 7 and 10 had the highest infection percentages and showed weakly negative or position correlations.

Environmental correlations between tree height and 1) number of limb galls, 2) number of limb plus stem galls, and 3) percent infected trees were small but consistently positive at ages 3 or 4 (Table 2). Within families, trees on the more favorable microsites grew more rapidly and had more infection than those on poor microsites. Presumably, rapid growth resulted in more foliage and more surface area for infection. At 10 years, however, the environmental correlations for these traits became negative or zero. Apparently the higher degree of infection on trees growing rapidly at young ages eventually caused their growth to slow down. Environmental correlations between height and frequency of stem galls at the young ages were 0 or negative, probably because stem galls can reduce growth rates even at early ages.

Although phenotypic correlations are not directly interpretive, they are presented in Table 2 for the sake of completeness, and because they are sometimes used in preparing selection indices.

An empirical view of some of the results clarifies relationships found and gives some idea of their magnitude. Test 8 at age 4 years showed pronounced microsite variation in both tree height and degree of infection. The block means for tree height and number of cankers per tree are shown in Figure 1. Note that trees in the west-central block had lowest average height (8.00 feet) and the least average number of cankers per tree (0.47). Blocks to the north, east, and south of this block showed increasingly greater growth and increasingly greater infection. Since all families were represented in all blocks, the pattern is essentially environmental.

Figure 2 depicts the effects of both the genetic and environmental correlations between tree height and gall frequency in test 8 at 4 years. The block means for the seven fastest growing families (selected on the basis of growth in tests other than those reported on here) are plotted along with the means for the seven slowest growing families. Note that, overall, galls per tree increased with increasing tree height, a reflection of environmental effects. But the most rapid growing families on the average had less infection for a given height than the slow growing trees. The fast growers averaged about 0.67 galls per tree, while the slow growers averaged 0.72 galls per tree. This difference is small, but after covariance adjustment to a common height for the effects of tree height, the difference increased, with the fast growers averaging 0.63 galls per tree and slow growers averaging 0.79 galls per tree.

Table 2.--Correlations between tree height and fusiform rust infection in slash pine.

	Type of correlation		
Test no.	Genetic [a]	Environmental	Phenotypic
	HEIGHT VS. LIMB GALLS AT 3 OR 4 YEARS [b]		
7	-.20(.31)	0.12	0.07
8	-.81(.15)	.11	.07
9	-.66(.22)	.13	.08
10	.24(.18)	.12	.14
	HEIGHT VS. STEM GALLS AT 3 OR 4 YEARS [b]		
7	.00	.05	-.04
8	-.10(.51)	.01	.01
9	-.56(.29)	-.01	-.04
10	-.05(.20)	-.19	-.17
	HEIGHT VS. LIMB + STEM GALLS AT 3 OR 4 YEARS [b]		
7	-.24(.38)	.09	.04
8	-.70(.22)	.10	.06
9	-.68(.21)	.12	.07
10	.19(.11)	.04	.07
	HEIGHT VS. PERCENT INFECTED AT 3 OR 4 YEARS [b]		
7	-.31	.16	.06
8	-.66	.33	.28
9	-.69	.18	.08
10	.15	.17	.16
	HEIGHT VS. PERCENT INFECTED AT 10 YEARS		
7	-.42	-.11	-.17
8	-.27	.05	.00
9	-.54	-.22	-.34
10	[c]	[c]	[c]

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[a] Standard errors of genetic correlations based on individual trees are in parentheses.

[b] At 4 years for tests 7 and 8, and at 3 years for tests 9 and 10.

[c] Test number 10 was not measured at 10 years.

Table 3.--Mean tree heights (families only) and degrees of infection by plantation and age.

	Age 3 or 4 a/			Age 10	
Test number	Height	Galls per tree b/	Infected tree c/	Height	Infected trees
	Feet	Number	Percent	Feet	Percent
7	9.2	1.02	48	30	64
8	8.8	.69	35	30	48
9	5.9	.72	34	29	64
10	5.1	1.10	52	d/	d/

a/ At 4 years for tests 7 and 8 and at 3 years for tests 9 and 10.
b/ Includes both stem and limb galls.
c/ Trees with either stem or limb galls.
d/ Test number 10 was not measured at 10 years.

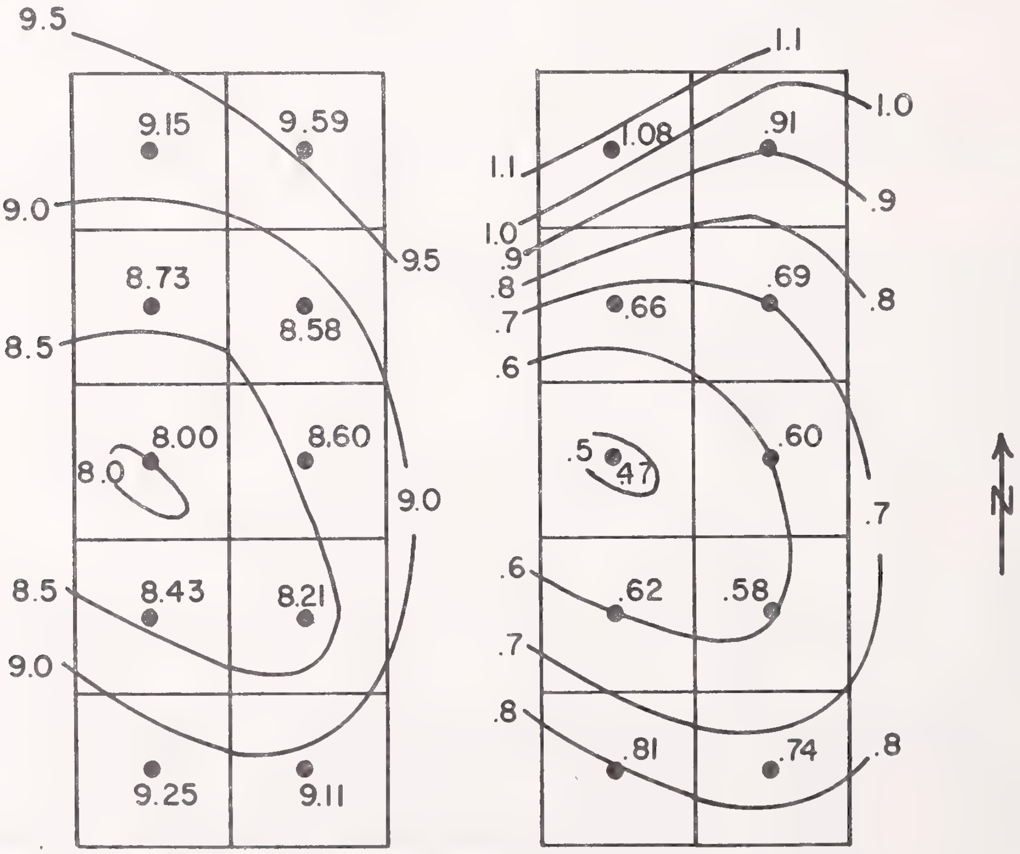

Figure 1. Correspondence between microsite variation of tree heights (in feet, left) with average number of galls per tree (right) in the 10 blocks in slash pine test 8 at 4 years. Values in centers of squares are block means.

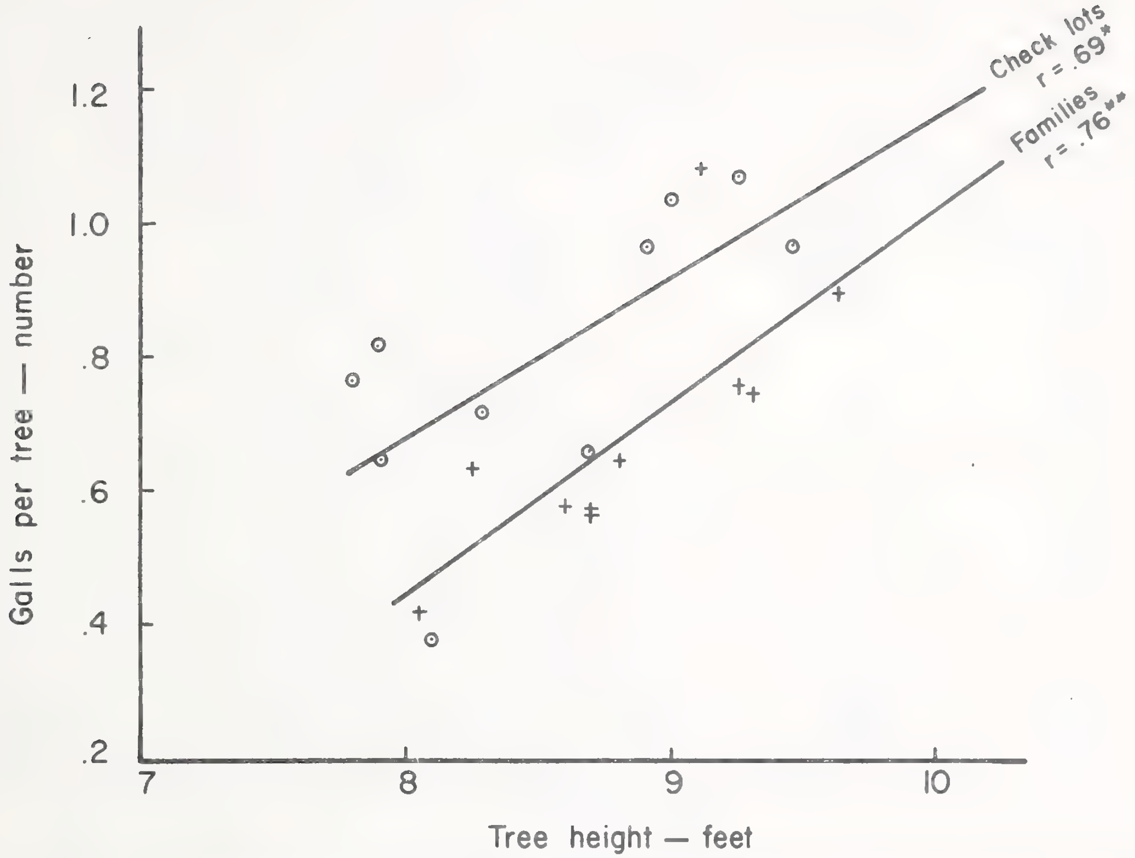

Figure 3. Replication means of number of galls per tree plotted over tree heights in slash pine test 8 at 4 years, for check lots (0) vs. families (+).

Although we used test 8 for making the above comparisons of the effects of selection, we also made computations for all tests (Table 4). Note that progeny of the faster growing parents usually had slightly lower infection percentages than those of poorest growers. Also, covariance adjustment usually increased the difference in infection between rapid and slow growers at the younger ages but not at age 10. Similar patterns were found when number of galls per tree was used as the measure of infection.

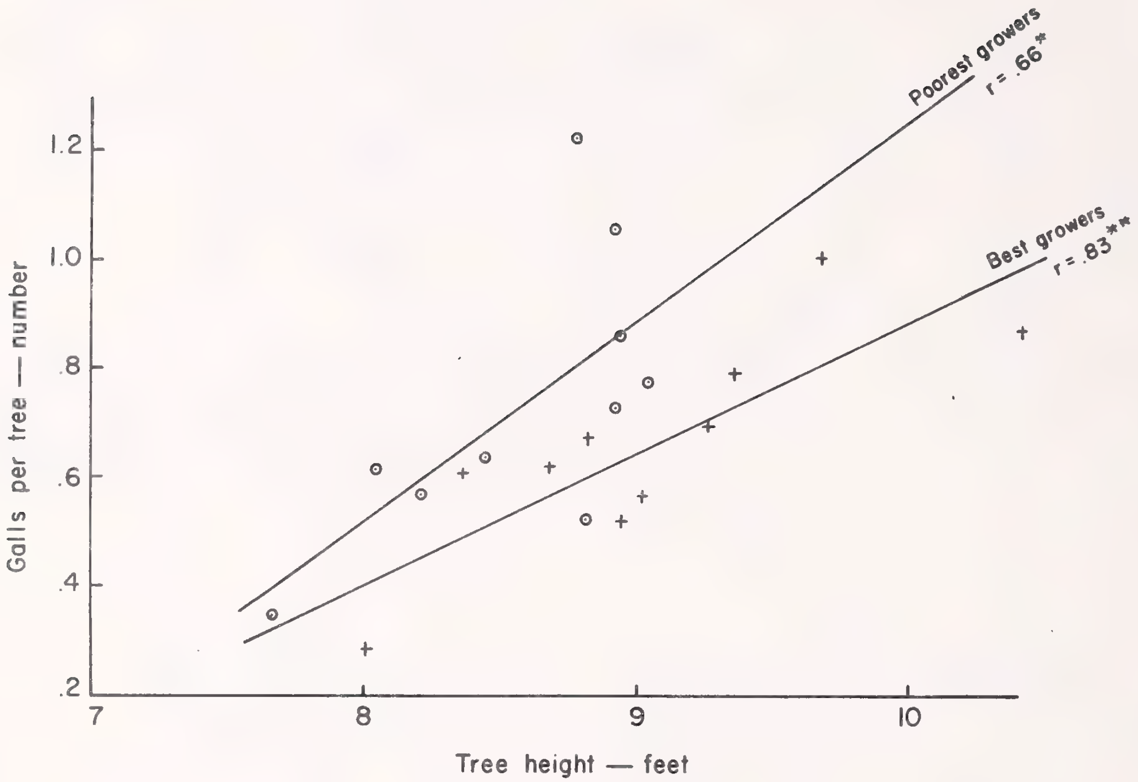

Figure 2. Replication means of number of galls per tree plotted over tree heights in slash pine test 8 at 4 years, for progeny of the poorest 1/3 parents selected for growth performance in other tests (O) vs. progeny of the best 1/3(+).

In the above analysis, the "selections" were made on the basis of performance in other tests in order to minimize the possibility of extraneous effects. That is, if we chose the trees on the basis of performance in Test 8, one could argue that in choosing the best growers we were essentially choosing those that had the least infection in this test, since infection can reduce growth rates. Actually, we made comparisons using both selection techniques and results were similar.

A similar comparison was made for check lots vs. families, again in test 8 at 4 years (Fig. 3). Since parents of the families were originally selected partly for rapid growth, they were expected to grow more rapidly than checks. Results, were essentially the same as those in Figure 2, with the check lots having more infection than families at given tree heights.

Table 4.--Effect of selection for growth rate [a] upon degree of rust infection before and after covariance adjustment for growth.

Family group	Percent infection at:			
	3 or 4 years [b]		10 years	
	Before adjust.	After adjust.	Before adjust.	After adjust.
		TEST 7		
Best 1/3	47	46	61	61
Poorest 1/3	47	48	64	66
		TEST 8		
Best 1/3	35	34	46	46
Poorest 1/3	37	37	48	49
		TEST 9		
Best 1/3	32	31	58	59
Poorest 1/3	38	38	70	66
		TEST 10		
Best 1/3	46	45	[c]	[c]
Poorest 1/3	59	59	[c]	[c]
Ave. best 1/3	40.0	39.0	55.0	55.3
Ave. poorest 1/3	45.2	45.5	60.7	60.3

[a] The best and poorest families were selected on the basis of parental evaluations made from tests other than those involved here.

[b] At 4 years for tests 7 and 8, and at 3 years for tests 9 and 10.

[c] Test 10 was not measured at 10 years.

CONCLUSIONS AND RECOMMENDATIONS

The negative genetic correlations found between growth rate and fusiform rust infection suggest that selection of trees for rapid growth will not cause a decrease in resistance and may even increase it slightly. The positive environmental correlations found at young ages mean that trees planted on sites favorable for growth are likely to incur more infection than if those same trees were planted on unfavorable sites. The latter conclusion agrees with findings by several investigators that stimulation of growth through cultural practices usually increases infection. Stimulation of growth, either through cultural means or by planting on sites favorable for growth, probably causes an increase in growing tips and foliage with an attendant increase in surface area for infection. But physiological effects may also be involved.

We recommend that tree breeders continue to select for rapid growth along with rust resistance when developing strains for planting on high rust hazard sites. We further suggest that when evaluating trees for rust resistance at young ages one should adjust for the effects of growth rate by covariance techniques. Adjustment at older ages may not be necessary.

Stimulation of growth through cultural practices in high rust hazard areas is another matter. Here the forest manager needs to weigh the costs of such practices, plus the expected increase in rust infection, against the expected gains in growth rate. From a long-term standpoint, we feel that it may be preferable to expand efforts to develop and utilize strains of trees superior in both growth and resistance.

LITERATURE CITED

Dorman, Keith W. 1976. The genetics and breeding of southern pines. USDA Forest Service. Handbook no. 471:407 p.

Falconer, D. S. 1960. Introduction to quantitative genetics. Ronald Press Co., New York: 365 p.

Helwig, J. T. and K. A. Council. 1979. SAS user's guide. SAS Institute, Inc. Cary, NC:494 p.

Rowan, S. J. and Klaus Steinbeck. 1977. Seedling age and fertilization affect susceptibility of loblolly pine to fusiform rust. Phytopathology 67:242-246.

OPERATIONAL PLANTATIONS OF IMPROVED SLASH PINE: AGE 15 RESULTS

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Abstract.--Paired commercial plantations of "improved" and "unimproved" slash pine were compared for volume production and fusiform rust infection at fifteen years from planting at ten locations in the Georgia Flatwoods. The "improved" trees were progeny of an unrogued clonal seed orchard, where the parents were phenotypically selected for volume production, crown and bole characteristics, and disease resistance.

Overall, the "improved" trees could not be shown to be any better than the "unimproved." Our inability to detect a significant difference between "improved" and "unimproved" slash pine may be due to the insensitivity of the test; we were only able to detect differences greater than ten percent in volume and 23% in rust infection. Additional sample stands could not be located and the realized gain from the earliest phenotypic selection practices may never be known.

Separate volume equations were derived for the "improved" and "unimproved" stock used in this study. These volume equations were not significantly different indicating that bole form was not altered by selection either.

Additional keywords: *Pinus elliottii*, realized gain, volume equations, fusiform rust, tree improvement.

INTRODUCTION

The first plantations of trees established from clonal seed orchard progeny are reaching merchantable sizes and only now can we begin to evaluate the real gains made from early selection methods.

In this study we examine the volume production and fusiform rust resistance of Union Camp's first slash pine "improved" plantations in comparison to adjacent nonimproved plantations. Only from such commercial plantations can actual realized gains be determined. Data was collected in the winter of 1981-82, fifteen years after establishment.

Measurements of this material at ages five years and ten years have been reported by Zoerb (1972, 1977). He recorded height, diameter, and fusiform rust infection finding that the improved trees were four percent larger in height and diameter, but that they had 34% greater rust infection at age five and 17% greater infection at age 10.

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In this update, we have sought to emphasize volume on a per unit area basis as a means for comparison. In order to do so, volume equations for improved stock had to be developed and compared to those for nonimproved stock.

The improved stock in this study are progeny from an unrogued clonal slash pine seed orchard, where the parents were phenotypically selected for volume production, fusiform rust resistance crown characteristics, and specific gravity. The results of this study apply only to "improved" populations derived from similar selection and propagation practices.

METHODS

Plot Measurements.

The study was made at 10 locations in the Georgia Coastal Plain (Figure 1) at each of which there was an improved and an unimproved stand. In each stand six .05 acre plots were established. Three of the six plots were selected according to the following criteria:

1. Minimal pest and pathogen evidence,
2. Minimal number of wild trees,
3. Minimal forked or otherwise deformed trees, and
4. Similar stand densities between improved and unimproved stands.

The other three plots were located randomly, adjacent to the three selected plots, to provide unbiased estimates of stand characteristics.

During the period fall 1981/winter 1982 measurements taken on dbh, total height, fusiform rust stem cankers were recorded for each tree.

Stem Analysis.

Two trees per plot were selected and felled for stem analysis. Selection of the sample trees was such that the range of dbh's over all the plots was represented in the sample. Diameters outside and inside bark were measured at the stump end and at 4 foot intervals along the stem, and the volumes of each 4-foot section was calculated using Smalian's formula. Individual tree volumes were obtained by summing the section volumes.

Tree Volume Functions.

Individual tree volume equations were derived for trees in both improved and unimproved stands to estimate stand volumes. The observed tree volumes from the stem analysis were used to determine least squares estimates of the coefficients in the model

$$V = b_0 D^{b_1} H^{b_2}$$

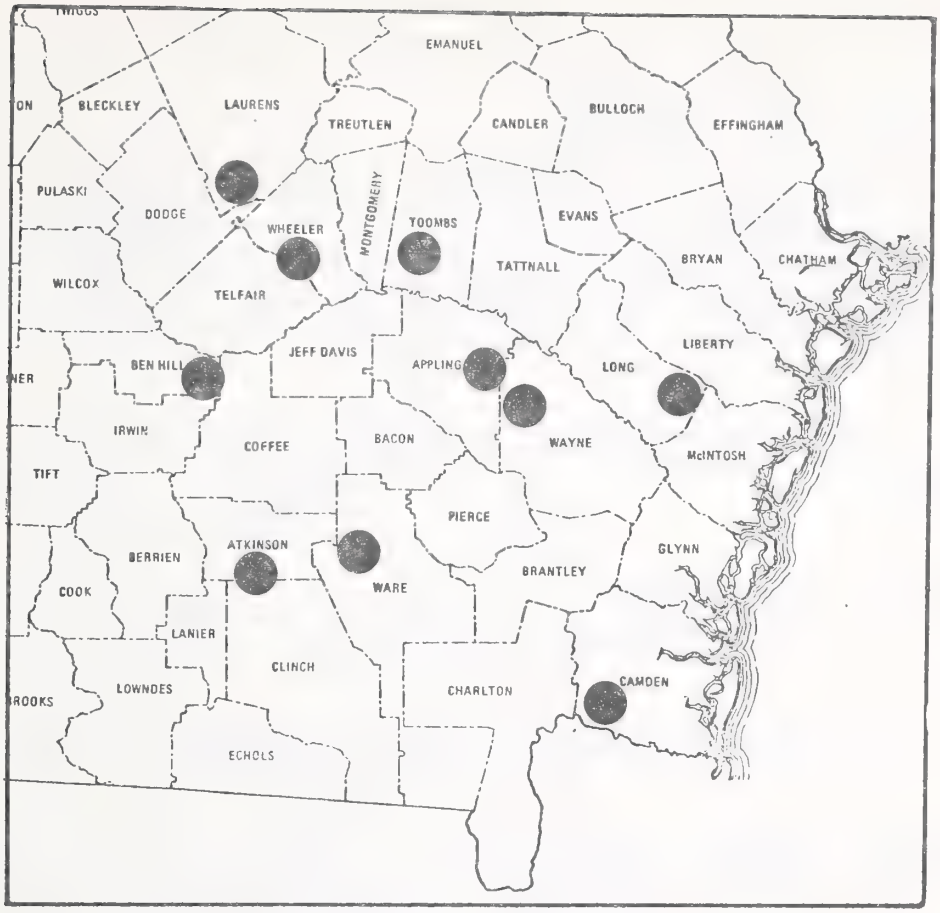

Figure 1.--Geographic location of sample plantations in Southeast Georgia.

where V = total stem volume (i.b. or o.b.) in cubic feet excluding stump
D = dbh in inches
H = total tree height in feet, and
b_0, b_1, b_2 = coefficients estimated from the observed data.

In addition, a taper function was derived from the above coefficients according to the methods of Clutter (1980).

Stand Volumes.

Stand volumes, on a per acre basis, were estimated by stand and stock tables in which the individual tree volume equations were applied to the diameter distribution on each plot.

RESULTS

Volume Characteristics.

Select versus random plots. At each location three improved and three unimproved plots were selected for comparison based primarily on equal plot density. Also three improved and unimproved plots were selected at random to provide unbiased comparisons of stand volumes and fusiform rust infection rates. However, the results from both kinds of comparisons were similar and the results that follow are, therefore, based on the pooled data.

Individual tree volume equations. The individual tree volume equations, both improved and unimproved, derived from the stem analysis, are shown in Table 1.

Table 1.--Estimated total cubic foot volume equations for 'improved' and 'unimproved' stands.

$$TCVOB_i = 0.0052897\ D^{1.9354216} H^{0.8741346}$$

$$TCVOB_u = 0.0068074\ D^{1.97604635} H^{0.78621135}$$

$$TCVIB_i = 0.0012254\ D^{1.9703507} H^{1.1384161}$$

$$TCVIB_u = 0.0013152\ D^{1.96456405} H^{1.11594819}$$

TCVOB = total stem cubic foot volume outside bark, excluding stump

TCVIB = total stem cubic foot volume inside bark, excluding stump

D = diameter breast height in inches
H = total tree height above ground level, in feet
i = 'improved'
u = 'unimproved'

The volume equations are graphed in Figure 2 which emphasizes their close similarity across the range of dbh's and heights found in these stands. The differences between improved and unimproved tree volume equations, both outside and inside bark, were tested in an analysis of covariance and could not be shown to be different at the five percent level (Table 2). This implies that the selection had no effect on tree taper either.

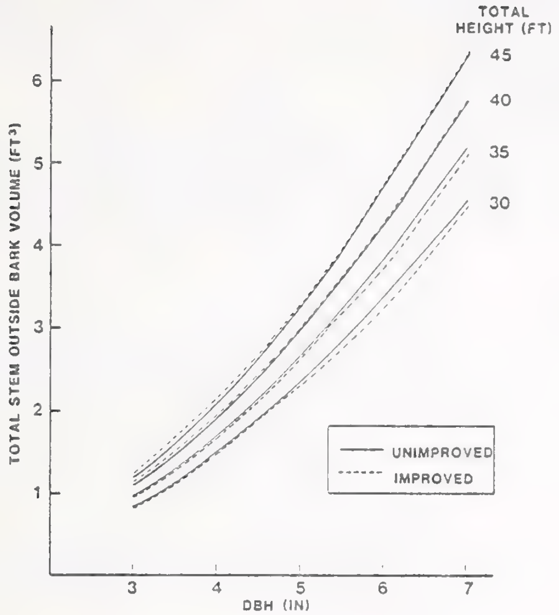

Figure 2.--Total stem: cubic foot outside bark curves for improved and unimproved slash pine.

Table 2.--Analysis of variance for testing seed source effects on volume equation 1.4.

		Outside Bark		
Source	df	MS	F	
lnDbh and lnTotHt	2	51.0318	17010.6**	
Seed Source	3	0.0019	0.633n.s.	R^2 = 0.9933
Error	234	0.0030	-	
Total	239			

		Inside Bark		
Source	df	MS	F	
lnDbh and lnTotHt	2	59.9479	8563.99**	
Seed Source	3	0.0091	1.3n.s.	R^2 = 0.9867
Error	234	0.0070	-	
Total	239			

Stand mean tree characteristics. The mean for all trees on the six improved and six unimproved plots at each location was calculated for dbh, total height, volume (inside and outside bark), and bark volume expressed as a percentage of total volume.

For each characteristic the difference between the improved and unimproved means was tested by a t-test at each location and by a paired t-test over all locations. The mean values are shown in Table 3 and significant differences at the five percent level are indicated by an asterisk.

In three of the ten locations the improved trees had significantly larger mean tree volumes while at one location the unimproved mean tree volume was greater. In general, the means for dbh and height follow the same pattern as mean tree volume. In seven out of the ten locations, however, bark percent was significantly less for the improved trees. At no location was mean bark percent greater for the improved trees.

The paired t-test over all locations showed no differences between the means with the exception of bark percent, where improved trees had a significantly smaller amount.

Stand characteristics. The stand characteristics, number of stems per acre, and volume per acre, inside and outside bark, were calculated at each location for the improved and unimproved stands, and the results are presented in Table 5.

The improved and unimproved means at each location were compared by t-tests. No differences were found at any location for these stand characteristics. Mean values over all locations could not be found to be different, either, using a paired t-test.

The number of stands available for this study was limited, and the inability to detect significant increases in volume may be due to the restricted sample size. With our sample size, we could detect a difference in volume per acre of ten percent (at the five percent level of probability). Sample sizes needed to detect smaller differences are shown in Table 5. About 40 pairs of stands would be needed to detect a difference of five percent in volume.

Fusiform Rust Infection.

Trees with fusiform bole cankers were recorded and the numbers expressed as a percentage of surviving trees at age 15. Mean infection rates for improved and unimproved stands are given for each location in Table 4. At each location the improved and unimproved infection rates were not significantly different.

Zoerb's (1972, 1977) five and ten year results show that the improved trees actually had greater fusiform infection. Our inability to show significant differences at age 15 may be due to greater mortality among the improved trees from rust infection at earlier ages.

Table 3.--Mean tree measures at sample locations.

Location	Seed Source	Dbh (in.)	TotHt (ft.)	TCVOB (ft^3)	TCVIB (ft^3)	Bark %
Appling Co.	I	5.3	40.4*	3.67	2.44	34.9
	U	5.5	42.2	4.04	2.66	35.0
Atkinson Co.	I	5.8	44.2	4.72*	3.22*	33.1*
	U	5.6	43.4	4.19	2.78	34.4
Ben Hill Co.	I	5.0	31.7	2.62	1.64	39.2
	U	4.8	32.5	2.49	1.51	40.4
Camden Co.	I	5.8*	44.7	4.63*	3.15*	32.9*
	U	5.4	43.4	4.04	2.70	34.4
Laurens Co.	I	5.4	36.6	3.62	2.37	36.6*
	U	5.8	37.2	4.10	2.62	37.8
Long Co.	I	4.6	32.2	2.42	1.52	39.2
	U	5.0*	34.4*	2.98*	1.88*	39.4
Toombs Co.	I	5.8*	38.2*	4.14*	2.72*	35.7*
	U	5.2	34.8	3.20	2.00	39.1
Ware Co.	I	5.2	41.4	3.62	2.40	34.4*
	U	5.2	41.4	3.51	2.30	35.5
Wheeler Co.	I	4.7	32.0	2.58	1.63	39.3
	U	4.9	34.2	2.70	1.68	39.4
Wayne Co.	I	4.9	38.8	3.03	1.98	35.8*
	U	5.0	37.7	3.07	1.96	37.4
Mean - All Locations	I	5.2	38.0	3.50	2.31	36.1**
	U	5.2	38.1	3.43	2.21	37.3

DISCUSSION

Realized gain in volume production.

To this point in time gains from improved southern pines have been estimated from small plot progeny tests. These results may be misleading when applied to commercial plantations, however. As Cannell (1982) points out, trees which grow largest in small plot progeny tests are superior competitors, and superior competitors may not produce maximal volume in large blocks, such as commercial plantations, because volume production on a stand depends more on the efficient use of limited resources rather than competitive ability.

Table 4.--Mean plot measures at sample locations.

Location	Seed Source	Stems/ Acre	Vol/Acre (ft^3)o.b.	Vol/Acre (ft^3)i.b.	Fusiform %
Appling Co.	I	456	1677	1115	27.3
	U	443	1792	1181	15.4
Atkinson Co.	I	476	2248	1535	16.8
	U	486	2041	1355	13.9
Ben Hill Co.	I	324	849	529	28.9
	U	376	937	570	12.9
Camden Co.	I	486	2252	1534	12.0
	U	520	2102	1402	8.2
Laurens Co.	I	250	905	592	60.4
	U	304	1243	794	73.8
Long Co.	I	350	849	534	16.1
	U	334	994	625	15.2
Toombs Co.	I	260	1076	707	45.2
	U	274	874	546	41.3
Ware Co.	I	486	1760	1171	5.8
	U	494	1734	1135	6.7
Wheeler Co.	(I)	174	447	282	35.9
	(U)	214	577	358	33.0
Wayne Co.	I	484	1466	959	13.2
	U	440	1350	862	10.6
Mean - All Locations	I	375	1353	896	26.2
	U	388	1364	883	23.1

Our primary purpose in this study was to determine realized gain from the earliest improved slash pine in commercial plantations rather than in small plot progeny tests and thereby also determine the actual effectiveness of the phenotypic selection practices used to assemble the improved parents. Unfortunately, our results are indefinitive. Because of the small number of stands available for sampling, we can say that the improved trees produced between ten percent more and eight percent less volume. Forty similar samples would be needed to detect the five percent improvement predicted from progeny test results (Ledig, 1973). To the best of our knowledge, however, the ten stands used in this study are the only ones of early vintage where improved and unimproved trees have been mapped separately.

Table 5.--Least significant differences and sample sizes estimates derived from data set.

Trait	Least significant difference (%)	Sample size needed to detect significant difference of: 5%	10%	15%
dbh	4.6	9	2	2
Total Height	3.4	5	2	2
TCVOB/tree	10.2	43	11	5
TCVIB/tree	11.2	51	13	6
Bark %	1.9	2	2	2
Stems/acre	5.9	14	4	2
TCVOB/acre	9.4	36	9	4
TCVIB/acre	10.3	43	11	5
Fusiform %	23.9	229	58	26

Although we were not able to meet our primary objective, more important is the fact that we may never be able to determine the gains made from the first round of phenotypic selection. This point may seem trivial now that we are well beyond this stage in the improvement of southern pines. However, because the southern pine breeding programs continue to be models for other breeding programs, it is imperative that we monitor the effectiveness of each procedure in the development of improved southern pines.

Differences in bark volume.

While no difference in wood volume was detected, the improved trees were shown to have significantly less bark volume (or thinner bark). Bark thickness was not a criterion for selection, nor is there any apparent biological association between bark thickness and any of the selection criteria (straightness, branch diameter, pruning, wood density, height, crown area/bole volume ratio, and disease resistance). The difference in bark thickness may be due to the geographic origins of the trees. The thinner-barked improved trees were from the moist Georgia-Florida flatwoods, while the thicker-barked unimproved trees were from the drier, and perhaps more fire prone, area around Emanuel County, Georgia.

Resistance to fusiform rust

When the first selections of slash pine were made, resistance to fusiform rust was not a major consideration. Trees with fusiform rust were not allowed, but most selections were made in stands with low infection rates. This amounted to *de facto* selection between stands. Results from this study and others (Goddard and Strickland, 1970, North Carolina State University, 1970, LaFarge and Krause, 1967) indicates that such practice was not effective. Phenotypic selection within heavily infected stands appears to be much more successful (Dinus, 1971).

CONCLUSION

This study is the first to investigate genetic gains in commercial plantations of southern pines. While the results are inconclusive, the need for future studies of this kind is evident. Testing of improved trees in large blocks is now widely practiced in southern pines and should yield more accurate estimates of gain made through genetic selection. However because these studies are designed to measure cumulative gain from several selection practices, the gain, in volume at least, from the early phenotypic selection practices may never be ascertained.

LITERATURE CITED

Cannell, M. G. R. 1982. 'Crop' and 'isolation' ideotypes: Evidence for progeny differences in nursery-grown *Picea sitchensis*. Silvae Genetica 31:60-66.

Dinus, R. J. 1971. Phenotypic selection for fusiform rust resistance. In Proceedings, Eleventh Conference on Southern Forest Tree Improvement. June 15-16, 1971, Atlanta, GA: 68-75.

Goddard, R. E., and R. K. Strickland. 1970. Cooperative Forest Genetics Research Program, 12th Progress Report. Univ. Fla. Sch. of For. Res. Rep. 18. 36pp.

LaFarge, T., and J. F. Kraus. 1967. Fifth-year results of a slash pine polycross progeny test in Georgia. Ninth South. For. Tree Improv. Conf. Proc. June 8-9, 1967, Knoxville, TN: 86-91.

Ledig, T. F. 1973. The application of mass selection in tree improvement. In 20th Northeastern Forest Tree Improv. Conf. Proc., July 31-Aug 2, 1972, Durham, NH. p. 69-82.

North Carolina State University. 1970. Cooperative tree improvement and hardwood research program, 14th Annual Report. N.C. State Univ., Raleigh, NC. 88pp.

Zoerb, M. 1977. Performance of nine and ten-year-old improved slash pine. Union-Camp Woodlands Res. Note No. 33. 3pp.

Zoerb, M. 1973. Performance of five and six-year-old improved slash pine. Union Camp Woodlands Res. Note No. 27. 5pp.

GENETIC VARIATION OF CONES, SEEDS, AND NURSERY-GROWN SEEDLINGS OF BALDCYPRESS (TAXODIUM DISTICHUM (L.) RICH.) PROVENANCES

Stephen Faulkner and John Toliver[1]

Abstract.--Genetic variation of baldcypress seed and cone characteristics and nursery-grown seedlings was explored through the use of two open-pollinated seed source collections made in the fall of 1980 and 1981. Source and family-within-source effects were significant for cone size and seed weight. Family-within-source was the only significant effect for number of seeds per cone and number of insect galls per cone. Differences in height and diameter growth were unrelated to source, but family differences were highly significant. The wide range of variability indicates a potential for genetic gain in the growth of baldcypress.

Additional keywords: Height growth, diameter growth, geographic variation, *Cecidomyiidae*.

Baldcypress (*Taxodium distichum* (L.) Rich.) is a commercial forest tree species commonly found in the bottomlands and swamps of the southern and southeastern United States. An estimated 155.7 million cubic meters of natural second-growth baldcypress is growing on commercial forest lands in the South (Williston et al. 1980). Much of this growing stock is of harvestable size or will attain such size within the next 25 years and cutting of these stands is increasing. These trees occupy vast acreages of permanently or periodically flooded sites and these low, wet sites are difficult to regenerate when harvested. In most cases, baldcypress may be the only commercial species that can be used to regenerate such sites. It is capable of fast growth and high-quality trees are in high demand for cypress lumber.

Little is known about regeneration or management of baldcypress. Natural regeneration is difficult to obtain making artificial regeneration a more feasible and viable alternative. The focus then shifts to finding the best genotypes for improved planting stock. While genetic variation in baldcypress is not well documented, there is limited evidence in the literature to support its existence (Beilman 1947, Correll and Johnston 1970, Flint 1974, McMillan 1974, Sharma and Madsen 1978). Information is presented here on the genetic variation of the cones and seeds of mature baldcypress trees and the height and diameter growth of one-year-old seedlings.

METHODS

Seed Collection

Two seed-source collections were made, one in the fall of 1980 (Collection I, 15 sources) and the second in the fall of 1981 (Collection II, 9 sources).

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These sources and their respective longitudes and latitudes are listed in table 1. Five individual parent trees were chosen from natural baldcypress stands located near each designated source. When possible, the selected parent tree was of the best form and vigor relative to other trees around it. However, due to a poor seed year in 1980, the selection criteria for Collection I was mainly finding a seed-bearing tree near the desired location. Twenty-five open-pollinated cones were collected from each parent tree, constituting a half-sib family.

Table 1.--Longitudes and latitudes of selected geographic seed sources of baldcypress - 1980 and 1981

Source	Location	Longitude	Latitude
		COLLECTION I - 1980	
1	Falfurrias, TX	90°10'	27°20'
2	Edgerly, LA	93°30'	30°15'
3	Simpson, LA	93°00'	31°15'
4	Stamps, AR	93°30'	33°20'
5	Quitman, LA	92°45'	32°20'
6	Woodworth, LA	92°30'	31°25'
7	Avery Island, LA	91°55'	29°55'
8	Pierre Part, LA	91°20'	30°05'
9	Lebeau, LA	91°35'	30°45'
10	Crossett, AR	91°55'	33°25'
11	Carbondale, IL	89°20'	37°05'
12	Stoneville, MS	90°55'	33°25'
13	Baton Rouge, LA	91°10'	30°30'
14	La Place, LA	90°30'	30°05'
15	Franklinton, LA	90°15'	30°55'
		COLLECTION II - 1981	
1	Natchez, MS	91°25'	31°35'
2	Alexandria, LA	92°30'	31°20'
3	Bogalusa, LA	89°50'	30°45'
4	Gibson, LA	91°00'	29°40'
5	La Place, LA	90°30'	30°05'
6	Stoneville, MS	90°55'	33°25'
7	Illinois/Kentucky	89°00'	36°55'
8	Monticello, AR	91°45'	33°37'
9	Bunkie, LA	92°10'	30°55'

Seed Handling

After collection, the cones were air-dried in a greenhouse and seeds were separated from the cones by hand. After cleaning and counting the seeds from Collection I, they were wrapped in heavy, porous nylon cloth to protect them from natural elements, and stratified by sinking them in a pond from February 19, 1981 to April 21, 1981 (61 days).

Following stratification, the seeds were planted from April 21, 1981 to May 5, 1981 in nursery beds in a compact family design following the procedure designated by Wright (1976). The design was replicated four times. All sources were randomized within each replication and families were randomized within sources. Approximately 40 seeds were planted per family per replication in rows 10 cm apart with 5 cm between seeds within a row.

Seed and Cone Data

The number of seeds per cone was the only seed/cone data taken for Collection I. All seeds, regardless of viability, were recorded as such; no effort was made to determine viability. While handling Collection I, numerous cone galls were observed. This led to recording the number of galls per cone for Collection II to determine if the number of galls per cone affected other variables.

The number of seeds per cone was recorded for Collection II. In addition, axil size (size of the cone in the same plane as the stem), cross-section size (size of the cone in the plane perpendicular to the stem), and individual seed weight were recorded. To determine seed weight, 25 cleaned seeds were randomly selected from a family within a given source and individually weighed on a Mettler balance to the nearest .1 milligram. Twenty-one out of 45 families were sampled this way.

Nursery Measurements

Germination counts for Collection I were made every two or three days following planting for a 41 day period. Germination was recorded when the hypocotyl broke through the soil surface. Height from groundline to the top of the terminal bud and diameter at groundline were measured after one growing season in the nursery.

Statistical Analysis

Analysis of variance was performed on the seed and cone data for both collections. The Statistical Analysis System (SAS) procedures ANOVA and GLM were used (Barr et al. 1979). Variance components were estimated with the SAS procedure NESTED and correlation coefficients were calculated to determine significant relationships between variables.

Due to highly variable germination compounded by severe damping off in the nursery beds, the number of seedlings per family within source was extremely unbalanced. Whole families were missing from many sources and complete sources were missing in replications II, III, and IV. After several unsuccessful attempts at conventional analysis, the decision was made to analyze the heights and diameters of seedlings from replication I only. Replication I was the most uniform with respect to missing families and sources, but was still unbalanced. Therefore, analysis of variance for unequal numbers of observations (using GLM) was performed on the height and diameter data for replication I. All four replications of germination data were analyzed.

Least squares means for heights and diameters of the families were calculated from the raw data. Least squares means are estimates of the expected arithmetic means if equal numbers of observations per class had been available (Barr et al. 1979).

RESULTS AND DISCUSSION

Seed and Cone Characteristics

Collection I.--Mean number of seeds per cone was 14. Values ranged from 2 to 30 seeds per cone. There were no significant source effects but family-within-source was significant at the .01 level of probability.

Collection II.--The mean number of seeds per cone was 17 with a range of 5-34 seeds. Family-within-source variation was the only significant effect (.01 level). A t-test indicated a significant difference at the .01 level of probability between the mean number of seeds per cone for Collection I (14) and Collection II (17). This indicates that in a poor seed year when fewer trees have cones on them those that do have cones have fewer seeds per cone. In both collections the average number of seeds per cone was lower than the average of 18-30 reported in the literature (Bonner 1974, Mattoon 1915).

The number of seeds per cone was positively correlated with axil size (r=.59) and cross-section size (r=.57), indicating the larger the cones, the greater the number of seeds. Mean axil size was 24.2 millimeters. Statistical analysis revealed significant source (.05 level) and family-within-source (.01 level) differences. Axil sizes ranged from 14.0 mm to 39.0 mm. Almost 20 percent of the variation in axil size was attributable to source of the cones while family-within-source was responsible for roughly 40 percent. There were no recognizable trends or patterns with regard to source effects on axil size. Mean cross-section was 24.6 millimeters (range 16.0-36.0 mm). Family-within-source was the only significant source of variation. As expected, cross-section size and axil size are highly correlated (r=.84).

Mean seed weight was 97.3 milligrams (range 36.2-196.5 mg). Seed weight was significantly affected by source (.05 level) and family-within-source (.01 level). Twenty-one percent of the variation in seed weight was due to source. However there was no apparent geographical trend. Family-within-source effects accounted for 24 percent of the variation. McMillan (1974) found source differences in the mean seed weights of baldcypress seeds collected from Illinois, Kentucky, Mississippi, Texas, and Mexico. Seeds from southern Texas and Mexico were the lightest, but this was attributed to interspecific variation father than geographic variation as T. mucronatum is the common cypress species of the area. Overall mean seed weight was 97.1 mg in that study. Seed weight was also influenced by size of the cone and the number of seeds per cone. Seed weight was positively correlated with axil size (r=.53), cross-section size (r=.52), and number of seeds (r=.17).

Research results have shown significant relationships between the weight of the seed and other characteristics such as germinative capacity, survival, and seedling size in many tree species (Korstian 1927, Perry and Coover 1933, Righter 1945, Shoulders 1961, Spurr 1944). With respect to baldcypress, it appears that by collecting larger cones (or selecting for large cone size in a breeding program), not only can the number of seeds be increased but seed weight and possibly germination and seedling size can be improved.

During seed handling of Collection I, numerous insect galls were observed inside the cones. The causal insect is probably a cone midge of the family Cecidomyiidae, possibly the same insect responsible for the familiar leaf gall on baldcypress. However, the taxonomy and identification are still uncertain, as are the mode of action and possible effects.[2] It appears that the larvae of the midge feed on the endosperm, hypocotyl, and radicle portion of the seed and possibly use the seed coat as material for the gall itself. Based on personal observations, it appears that the seeds next to the gall are generally devoid of a solid embryo, misshapen, and lighter.

The mean number of galls per cone was 8. This is almost 50 percent of the mean number of seeds per cone. The number of galls per cone ranged from zero to 40 and varied significantly among parent trees. There were no significant differences in number of galls per cone among sources.

Just what effect these galls have on baldcypress seed viability remains to be seen. There was no significant correlation of galls with the total number of seeds per cone. When seed counts were made, anything recognizable as a baldcypress seed was counted and no effort was made to determine viability even though there were obvious physical differences in appearance. Distinguishing between viable and non-viable seed may provide different results.

The number of galls per cone was negatively correlated with seed weight ($r=-.40$) in that lower seed weights were associated with higher number of galls. It is apparent that the causal insect utilizes or removes some portion of the seed in the production of the gall or causes a reduction in embryo size, thus reducing seed weight. This could impact germination values or seedling sizes in light of the literature discussed in the section on seed weights. It seems prudent that when collecting seed with numerous cone galls, an effort should be made to collect extra cones to insure an adequate amount of usable seed.

Germination

Overall germination in the nursery was poor, with a mean germination of 15.5 percent (range 0.0-80.0%). Results of previous studies show ranges in germination of 25 to 75 percent (Beilman 1947) and 40 to 60 percent (Mattoon 1915); Bonner (1974) reported 74 percent germination in laboratory tests based on full seeds only. Seeds in this study were not chosen by this criterion, although an effort was made to discard obviously inviable seed. Germination data, as well as height and diameter data, were taken on Collection I only. The low overall germination is probably a result of the generally poor quality of the seed. The high germination figures for some families (70 to 80 percent) would indicate that there was nothing wrong with the stratification procedures or germination conditions.

There were significant differences in percent germination due to source as well as family-within-source at the .01 level. Fifty percent of the variation in germination was due to source, while 28 percent was due to family-within-source. Families from La Place, Louisiana, had the highest mean germination (45.8 percent) and were significantly different from the other sources, however there was no particular geographical trend.

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[2] Personal communication with Dr. Richard Goyer, Associate Professor of Entomology, Louisiana State University.

Height and Diameter of Seedlings After One Growing Season in the Nursery

Height.--The mean height for all seedlings was 81.4 centimeters. There were no significant source effects but family-within-source variation was significant at the .01 level of probability. The family with the tallest seedlings was from Avery Island, Louisiana, and the mean family height was 104.3 cm. The family with the shortest seedlings (52.6 cm) was also from Avery Island (table 2). This wide range in height growth between two families from one source and the large amount of family variation indicates a high degree of genetic diversity among individual trees in natural stands of baldcypress. The mean height growth of the top ten percent of the families was 99.4 cm a 22.5 percent gain when compared to the overall mean height of 81.4 cm.

Table 2.--Least squares means in centimeters for diameter and height of one-year-old baldcypress seedlings by source and family

SRC[1]	FAM	DIA	HT	SRC	FAM	DIA	HT	SRC	FAM	DIA	HT
7	5	1.9	104.3	11	4	1.2	79.3	10	2	1.0	79.9
13	3	1.8	83.0	11	2	1.2	98.4	12	4	1.0	87.4
1	2	1.7	87.3	12	5	1.2	89.5	8	5	1.0	80.9
3	2	1.6	87.2	11	3	1.2	77.6	11	5	1.0	73.2
4	1	1.5	80.0	6	5	1.2	91.5	14	3	1.0	78.2
7	4	1.5	96.7	6	2	1.2	75.0	10	3	1.0	77.6
13	5	1.5	100.8	4	5	1.2	78.0	8	2	1.0	76.0
4	4	1.5	77.0	3	4	1.2	80.0	6	4	1.0	60.0
5	5	1.4	100.0	3	3	1.2	82.0	14	2	1.0	82.4
5	2	1.4	75.8	2	4	1.2	84.7	15	2	2.0	73.5
7	2	1.3	96.0	9	4	1.2	70.3	12	2	0.9	83.5
1	3	1.3	92.8	11	1	1.2	92.4	14	4	0.9	78.4
3	1	1.3	90.0	2	1	1.2	75.7	8	4	0.9	71.6
4	2	1.3	74.0	2	3	1.2	78.4	12	1	0.9	67.3
9	5	1.3	83.8	13	4	1.2	68.5	1	4	0.9	57.0
14	1	1.3	86.5	10	4	1.1	86.2	10	5	0.9	76.0
3	5	1.2	85.0	9	2	1.1	92.5	8	1	0.9	67.2
2	2	1.2	90.1	15	1	1.1	80.2	10	1	0.8	75.2
9	1	1.2	88.9	14	5	1.1	90.1	12	3	0.8	77.3
4	3	1.2	76.4	2	5	1.1	71.4	7	1	0.8	52.6
5	3	1.2	73.2	7	3	1.0	64.5				

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[1] SRC = source, FAM = family, DIA = diameter, HT = height.

Selection of families with an ability to make rapid early height growth is especially important in establishing baldcypress plantations. In areas subject to flooding, keeping the tops above the water line is necessary to insure survival. Baldcypress also appears to be non-competitive with annual weeds and brush. The taller a seedling when planted, the greater the advantage it will have with competing vegetation. By planting seedlings from superior families, survival should improve, cultural treatments (i.e. disking, mowing) could be reduced, and, possibly, the rotation period would be shortened.

Diameter.--The mean ground-line diameter for all seedlings was 1.1 cm. Source effects were not significant, but family-within-source was highly significant. The family with the largest mean diameter (1.9 cm) was from Avery Island, Louisiana and was also the family with the tallest seedlings (table 2). This is not surprising as height and diameter were found to be highly correlated (r=.75). At 0.8 cm, members of the family with the smallest mean diameter were also from Avery Island.

The same opportunities for exploiting the wide genetic diversity in baldcypress to improve early height growth exist for diameter growth, but on a larger scale. The top ten percent of the families have a mean diameter of 1.6 cm. This represents a 50 percent gain in diameter growth over the grand mean for all families of 1.1 cm.

There is a high degree of family variation in early height and diameter growth for baldcypress. Thus parent tree selection by progeny testing should yield a good opportunity for genetic gain.

SUMMARY AND CONCLUSIONS

There was very little evidence of geographic variation exhibited by one-year-old baldcypress seedlings in the nursery. No source variation was found for height and diameter growth. Mean seed weight and germination were significantly affected by source. It is probable that the scope of this study was not large enough to detect geographic variation, as this was a limited-range study relative to the natural range of baldcypress. However, the lack of geographic variation could also be due to the similarity of the sites on which it is found throughout its natural range.

Seed and cone characteristics showed significant family variation and significant relationships between the size of the cones and the number of seeds per cone. The number of seeds per cone was lower than that previously reported. In addition, the number of galls per cone and seed weight were negatively correlated.

The high degree of family influence on the genetic variability of height and diameter growth indicates a potential for genetic gain in the growth of baldcypress. However, progeny testing in the field for longer periods of time must be completed before reliable data can be obtained.

LITERATURE CITED

Barr, A. H., Goodnight, J. H., Sall, J. P., Blair, W. H., and Chilko, D. M. 1979. SAS user's guide, 1979 ed. SAS Institute, Inc., Cary, N.C. 494 p.

Beilman, A. P. 1947. What happens when all kinds of southern cypress are grown in the north? South. Lumberman 174(2179):48.

Bonner, F. T. 1974. In C. S. Schopmeyer (ed.) Seeds of woody plants in the United States, p. 796-798. USDA For. Serv. Agric. Handb. No. 450.

Correll, D. S., and Johnston, M. C. 1970. Manual for the vascular plants of Texas. Texas Research Foundation. 1188 p.

Flint, H. L. 1974. Geographically based physiological variation in Taxodium distichum (L.) Rich. Hortscience 9(3 sec 2):301 (abstract).

Korstian, C. F. 1927. Factors controlling germination and early survival in oaks. Yale Univ. Sch. For. Bull. 19:92-96.

Mattoon, W. R. 1915. The southern cypress. USDA Bull. No. 272, 74 p.

McMillan, C. 1974. Differentiation in habitat response in Taxodium distichum, Taxodium mucronatum, Platanus occidentalis, and Liquidambar styraciflua from the United States and Mexico. Vegetatio 29:1-10.

Perry, G. S., and Coover, C. A. 1933. Seed source and quality. J. For. 31:19-25.

Righter, F. I. 1945. Pinus: The relationship of seed size and seedling size to inherent vigor. J. For. 43:131-137.

Sharma, G. K., and Madsen, L. 1978. Variation in baldcypress from different habitats. J. Tenn. Acad. of Sci. 53(3):115-116.

Shoulders, E. 1961. Effect of seed size on germination, growth, and survival of slash pine. J. For. 59:363-365.

Spurr, S. H. 1944. Effects of seed weight and seed origin on the early development of eastern white pine. J. Arnold Arbor. 25:467-480.

Williston, H. L., Shropshire, F. W., and Balmer, W. E. 1980. Cypress management: a forgotten opportunity. Southeast Area, State and Private For., USDA For. Serv. For. Rep. SA-FR8, 8 p.

Wright, J. W. 1976. Introduction to forest genetics. Academic Press, New York. 463 p.

ACCELERATED BREEDING AND EARLY SELECTION

MAXIMIZING GENETIC GAIN IN LOBLOLLY PINE BY APPLICATION OF ACCELERATED BREEDING METHODS AND NEW CONCEPTS IN ORCHARD DESIGN

Michael S. Greenwood[1]

Abstract.--Despite advances in cloning, seed orchard seed as a significant source of genetically improved loblolly pine will be of importance indefinitely. Increasing genetic gain per unit time can not only be accomplished by decreasing the time needed for breeding and testing, but also by improving the yield of existing seed orchards, both in terms of quantity and genetic composition. Clonal orchard blocks as a means to this end should be seriously considered on an experimental basis.

Additional Keywords: Improved seed, juvenility, pollen contamination, supplemental mass pollination.

INTRODUCTION

Borlaug (1983) points out that there are still tremendous gains to be made by conventional breeding of essential food crops, and that genetic engineering combined with large-scale multiplication by tissue culture still faces formidable technical and biological obstacles. I suggest this is even more true in forestry, where we have only begun to plant the progeny of our first-generation selections, most of which derive from totally wild ancestry. Despite promising results in the field of woody plant tissue culture (e.g., Farnum et al, 1983), woody perennials that root poorly are probably the hardest plants of all to clone. In addition, woody perennials (including loblolly pine, Greenwood, unpublished data, 1983) undergo phase change, or maturation, which must be dealt with if cloning is to capture the gains considered theoretically possible. While I support research in cloning forest trees, the numerous obstacles facing clonal propagation must be dealt with patiently and thoroughly, to avoid the risk of forcing premature implementation of flawed technology.

Even if cloning were available today, it probably would not be cost effective or wise to regenerate a given company's acreage with only clonal material. Seed orchard-produced seed will continue to provide significant quantities of seed for regeneration purposes, perhaps indefinitely. Therefore, we must not neglect efforts to extract all the gain possible out of our current sexually-based seed production systems since our seed orchards represent a large investment.

This paper will briefly review some ways that genetic gain increment per

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Table 1.--Time periods (in years) for critical steps in a loblolly pine breeding and seed production program, assuming three different levels of implementation of new technology. Assume minimum of thirty clones for a new production orchard.

	Technology	•Traditional Field Breeding & Testing	•Accelerated Breeding Facility	•Accelerated Breeding •Earlier Selection •Clonal Blocks
A	Selection Age	8	8	2 - 8, avg. 5
B	Breeding period from grafting to test establishment	12[+]	5	5
C	Gen. Turnover (A+B)	20	13	7 - 13, avg. 10
D	Time to full production (includes gap for selection period)	15	15	12[*]
E	Comparison Factor $\frac{A + B + D}{35}$	1.0	0.77	0.63

[+] Includes 1 y for grafting, 4 y until both ♂ , ♀ produced, 5 y for breeding and 2 y for cone maturation.

[*] Three years saved because new clones can be established immediately, instead of waiting until enough selections have been made for a new orchard.

unit time can be maximized. More precise, and/or earlier selection methods will be discussed in the following paper (Lambeth, 1983, these proceedings). Here we will touch on some ways we can increase genetic gain increment per unit of time. Included will be methods currently in use to increase the rate of generation turnover, a discussion of a possible stumbling block regarding flower induction, and a proposal for further improvement involving the establishment of seed orchards in clonal blocks. This last item will require control of pollination, but will increase gain per unit time.

The advantages of controlling pollination in seed orchards have been discussed before (Denison & Franklin, 1975; Sweet and Krugman 1977; Bridgwater and Trew, 1981). The consequences of not controlling pollination have also been discussed (e.g., O'Reilly et al 1982); there is little doubt that mating is not random among clones in a wind-pollinated seed orchard. In addition, there is evidence for the existence of large amounts of background contamination (e.g., Squillace and Long, 1980; Adams and Smith, 1983; these proceedings).

SHORTENING GENERATION TURNOVER

The generation turnover interval can be shortened both by lowering the selection age and by decreasing the breeding period (see Table 1). We have reduced the breeding period by applying flower stimulation procedures which have been described in detail elsewhere (Greenwood, 1978, 1981 and 1982). Tree improvement facilities are being developed by several companies in the South where the flower promoting effects of greenhouse culture, treatments such as water stress plus Gibberellin $A_{4/7}$, and out-of-phase dormancy can be applied. The impact of early flowering technology on the generation turnover interval is shown in Table 1. Further discussion of these techniques would be redundant here, but given the interest in trying to develop selection methodology that could be applied as early as two years from seed, the effects of juvenility on flowering may provide a stumbling block for flower induction. Table 2 shows the effects of ortet age on the flowering of grafted material.

Table 2. The effect of ortet age on flowering (3 growing seasons after grafting) by loblolly pine scions from five half-sib families.

	Age of Scion Donor, Years			
	1	4	8	12
♀ strobili per tree	.41 a	1.00 b	1.17 b	2.32 b
♂ clusters per tree	.02 a	.97 b	.87 b	2.58 b

Previous flowering results from these scions have already been reported (Greenwood, 1981) which show no male or female flowering after two growing seasons by scions from ortets aged one year. After an additional year of greenhouse culture but no other flower stimulation treatment other than water stress, flowering did occur on the scions from one-year-old ortets, but it was still significantly ($p \leq .05$) less than that observed with ortets aged four or more. Although the amount of both male and female flowering increases progressively with age, the biggest difference in flowering is observed on scions from ortets aged 1 and 4. This is especially true for male flowering, where almost a fiftyfold increase was noted between these ages. Apparently reproductive maturation is most rapid between ages 1 and 4, but appears to increase steadily, though less rapidly thereafter. Flower stimulation treatments could not completely compensate for decreasing scion age (Greenwood, 1981). Therefore, if selections are made as early as two years from seed, some allowance must be made for their flowering less well. Poor flowering could offset the benefit of selecting at such an early age, by forcing the establishment of larger breeding orchards, or waiting longer to complete breeding. Further work to see how much reproductive maturation occurs between ages 1 and 2 or 1 and 3 would be useful.

CLONAL ORCHARD BLOCKS

Establishing future orchards in clonal blocks offers two major opportunities to increase the amount of gain per unit time, which include:

(A) mandatory use of artificial pollination, which will offset deleterious effects of background pollen and which will produce the most desirable matings as indicated by genetic testing.

(B) earlier establishment of new clones, which will decrease the time until adequate quantities of seed are available.

In addition, clonal blocks might be more efficient from the standpoint of seed orchard management, especially for cone harvest, fertilization, insect control and roguing.

Supplemental mass pollination (SMP) has been tried numerous times on Pinus, and the results have been reviewed by Bridgwater and Trew (1981). Although no one to date has reported a high rate of success, both Koski (1975) and Sweet (1977) mention that female receptivity (in Scotch and Radiata pine) occurs prior to bulk of pollen flight, either from the orchard or surrounding areas. We have made similar observations in our seed orchards (see Figure 1), noting that the female strobili of a subsample of five clones become receptive well before the majority of background or orchard pollen flies. If we assume that pollination can be effective at stage 4, as has been shown by Bramlett and Matthews (1983, these proceedings), then there is clearly not only an opportunity for supplemental mass pollination prior to orchard pollen flight, but also for background pollen to successfully compete with orchard pollen. Working with dyed pollen, Bridgwater and Williams (1983, these proceedings), have shown that the majority of the pollen reaching the nucellus can be applied artificially, without in any way protecing the flowers. They conclude that SMP is feasible, if enough pollen can be applied. If they are correct, then operational SMP should be possible, which would allow the establishment of future seed orchards in clonal blocks.

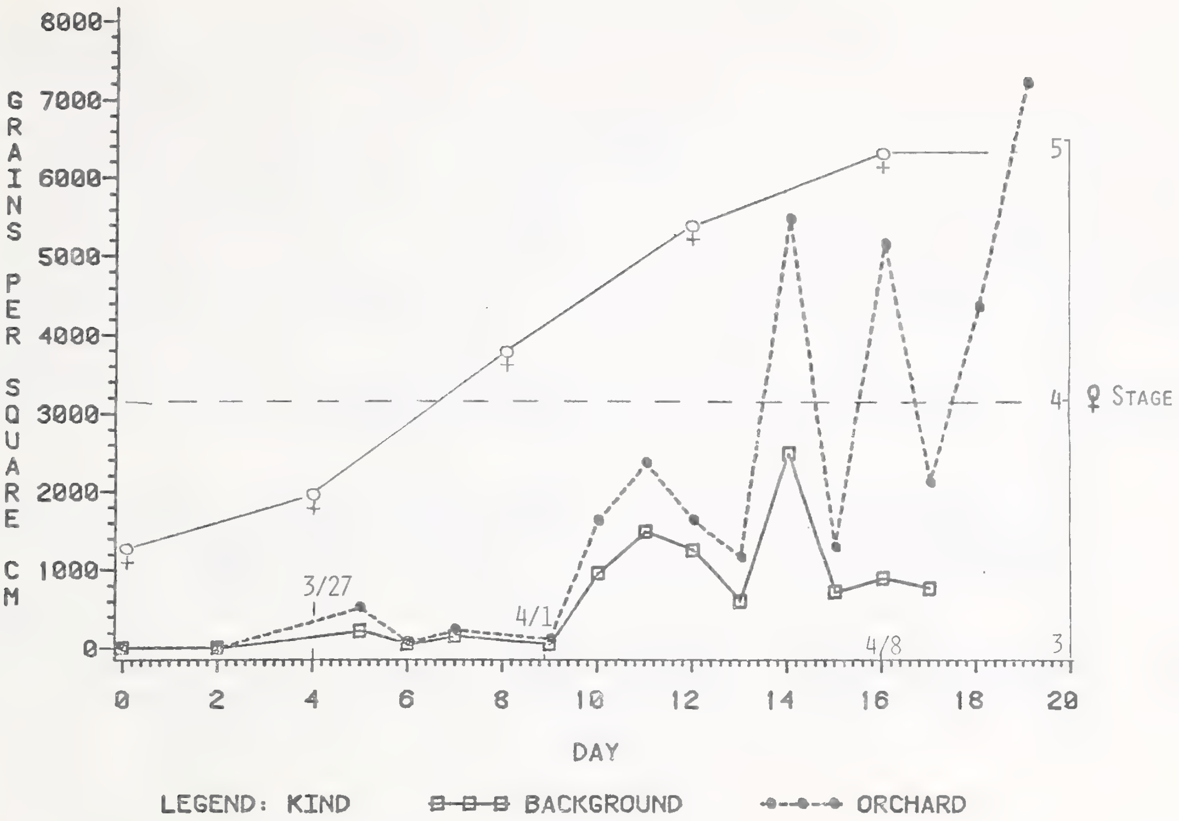

Figure 1.--Pollen flight (in grains/cm^2/24h, average of 10 traps inside orchard, 5 outside) and average female stage (for 5 clones) by day at the J. P. Weyerhaeuser Seed Orchard, Spring, 1983.

An orchard consisting of clonal blocks can be managed so that gain per unit time can be increased by prompt replacement of clonal blocks whenever a superior clone can be identified through genetic testing. At present, the North Carolina State Co-op recommends 20-40 clones for the establishment of a new seed orchard, with a conventional, randomized design. Since neither crossing nor genetic test establishment can be carried out in one year, nor can all potential selections be made precisely in a given test at one time, the clones for a given orchard will become available over a period of about 7 years. Thus, seven or more years will elapse before enough selections have accumulated to establish the orchard, and valuable time is lost in obtaining seed production. If, instead, the orchard were established in clonal blocks, each clone could be grafted immediately after selection, and established in the orchard as soon as possible thereafter. In succeeding generations, there would be no need to establish an entire new orchard; instead, the new clones of the next generation could be established promptly where clones of the previous generation had been rogued out.

DISCUSSION AND CONCLUSIONS

Table 1 shows what I consider to be key components (A-D) in maximizing genetic gain per unit time. Shortening any one of these will increase the amount of genetic gain per unit time. The last row presents a comparison factor for the three alternatives presented, and consists of the sum of the selection age, breeding period and the time to full production for the seed orchard, divided by the sum of the same components for the "traditional" breeding and testing program. The factors allow a quick comparison of different alternatives to obtaining gain faster. While all three cases are hypothetical, the first two probably resemble some actual scenarios, while the third case assumes early selection and orchard establishment in clonal blocks, which knock about three years off the eight-year selection period, and three years off the time to full production due to earlier establishment of selections.

I am advocating only that clonal block establishment be considered from a research standpoint, with the hope some day soon that practical SMP becomes a reality. The disadvantage of clonal block design obviously would be increased selfing if SMP were not done, or were ineffective. The resultant decrease in seed yield or decreased progeny performance due to inbreeding depression would not be acceptable. However, the table does show that there are numerous opportunities for increasing genetic gain per unit time, especially in the areas of selection age and time to full production in the seed orchard.

LITERATURE CITED

Borlaug, N. E. 1983. Contributions of conventional plant breeding to food production. Science 219, 689-693.

Bridgwater, F. E. and I. F. Trew. 1981. Supplemental Mass Pollination. In: Pollen Management Handbook, U.S.D.A. For. Sci. Agi. Handbook #587, pp. 52-57.

Denison, N. P. and E. C. Franklin. 1975. Pollen Management. In: Forestry Commission Bul. #54, R. Faulkner, Ed. London, U.K. Pp. 92-100.

Farnum, P., R. Timmis and J. L. Kulp. 1983. Biotechnology of Forest Yield. Science 219, 694-702.

Greenwood, M. S. 1978. Flowering induced on young loblolly pine grafts by out-of-phase dormancy. Science 201, 443-444.

Greenwood, M. S. 1981. Reproductive Development in Loblolly Pine. II. The effect of age, Gibberellin plus water stress and out-of-phase dormancy on long shoot growth behavior. Amer. J. Bot. 68, 1184-1190.

Greenwood, M. S. 1982. Rate, timing and mode of gibberellin application for female strobilus production by grafted loblolly pine. Can. J. For. Res. 12, 998-1002.

Koski, V. 1975. Natural pollination in seed orchards with special reference to pines. In: Forestry Commission Bul. 454, R. Faulkner, Ed., London, U.K. Pp. 83-91.

O'Reilly, C., W. H. Parker and J. E. Barker. 1982. Effect of pollination period and strobili number on random mating in a clonal seed orchard of *Picea mariana* Silv. Gen. 31, 90-94.

Squillace, A. E. and E. M. Long. 1981. Proportion of pollen from nonorchard sources. *In:* Pollen Management Handbook, U.S.D.A. For. Ser., Agr. Handbook #587, pp. 15-19.

Sweet, G. B. 1977. A new concept of *Pinus radiata* seed orchards. What's new in Forest Research, #49 (May) Forestry Research Inst., Rotorua, New Zealand.

Sweet, G. B. and S. L. Krugman. 1977. Flowering and seed production problems and a new concept of seed orchards. Proc. Third World Conference For. Tree Breeding, Canberra, Australia, CSIRO, March 21-26. Pp. 749-759.

EARLY TESTING - AN OVERVIEW WITH EMPHASIS ON LOBLOLLY PINE

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Abstract.--"Early testing" for growth rate has the potential to reduce the generation cycle in loblolly pine by 4-8 years as compared to conventional field testing, though it is not yet on operational procedure. Research in this area has been hampered by a scarcity of well-designed and economically mature genetic tests by which the "early test" is gauged and sampling problems associated with characterizing family rank correlations between experiments when heritabilities are low to moderate.

Nonetheless, there are sufficient positive results from recent studies to warrant the establishment of experimental populations where "early testing" and accelerated breeding are used to cycle populations through generations as rapidly as possible to determine the validity of the procedures. A six- or seven-year cycle is possible.

Techniques in "early testing" for fusiform rust resistance and drought resistance have been developed and are currently in practice. Other adaptability traits lend themselves well to "early testing".

INTRODUCTION

The reality of reducing the breeding-testing cycle by conducting selection at very young ages has, by and large, escaped the forest geneticist though the hope still remains. Recent and successful techniques to induce early flowering have greatly reduced the breeding phase of the generation cycle in loblolly pine but for over a decade there has been little change in the duration of the testing phase. Most operational programs are based on 5 to 10-year-old selections from genetic tests.

"Early testing" is usually pictured as a process whereby trees are selected after being grown at close spacing in a greenhouse, growth chamber, or nursery for one or two years. Such testing has the potential to increase genetic gain per year by significantly shortening the generation cycle if family ranks in the "early test" are reasonably consistent with those in longer-term field tests. Furthermore, an "early test" would considerably increase the payoff for tree improvement investments by greatly reducing testing costs and the time required to capture genetic gains in production orchards.

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Because "early testing" has tremendous potential to impact tree improvement efforts, if successful, it is paramount that research in this area be reviewed periodically for potential applications and to generate new ideas for research emphases.

HOW LARGE A CORRELATION?

As is often the case in scientific inquiry, "early testing" is considered "guilty until proven innocent". That is, until it is shown to be workable, or at least better than conventional testing, it will receive little use. As will be shown, proving the "innocence" of "early testing" is not a simple task even if such is the case. The question is: How strong a genetic correlation between the "early test" and later performance is needed to make "early testing" a workable procedure? To compare the effectiveness of "early testing" with selection at mature ages requires a look at their genetic gain equations. The gain (G_M) from direct selection at maturity (economic rotation age) is expressed as:

$$G_M = i_M h_M^2 \sigma_M^2$$

while the correlated gain in the mature trait from selection on a juvenile trait (sometime before maturity) is (Falconer, 1960):

$$CG_M = i_J h_J h_M r_{J,M} \sigma_M,$$

Where: J, M = subscripts that denote the juvenile or mature trait
i = selection intensity
h^2 = heritability
r = genetic correlation
σ = phenotypic standard deviation.

To determine the gain per year for each of these testing schemes requires that each be divided by T, the number of years to complete a cycle. The efficiency (E) of "early testing" as compared to testing to maturity is therefore:

$$E = \frac{CG_M/T_J}{G_M/T_M} = \frac{i_J h_J r_{J,M} \sigma_M T_M}{i_M h_M^2 \sigma_M T_J} = \frac{i_J h_J r_{J,M} T_M}{i_M h_M \quad T_J}$$

If E = 1 then equal gain per year will be realized with either scheme. In fairness though, an economic analysis is required to determine their relative values. Indeed, this is how the efficiency of "early testing" should be assessed. Working against "early testing", in an economic sense, is the fact that breeding and testing must be repeated several times during one mature selection cycle. On the other hand, some increment of gain is realized after the first "early testing" cycle and in small increments for subsequent generations, whereas with mature selection no incremental gain is realized for many years.

For the sake of argument some simplifying assumptions will be made. Assume

$i_J = i_M$,

$h^2_J = h^2_M$,

T_J = selection age (2 years) + 5 years to breed = 7 years,

and T_M = selection age (30 years) + 5 years to breed = 35 years.

In reality, the selection intensity for the "early test" (i_J) should be greater than i_M since more of the smaller plants could be tested in a given amount of space, therefore, this assumption works in favor of mature selection in calculations of E. The impact of the assumption regarding equal heritabilities is unknown but it does not seem unrealistic although h^2_J could conceivably be manipulated by the proper choice of "early test" environment which reduces environmental variance and thus increases h^2_J. The generation cycles, T_J and T_M, are based on a 2-year nursery test versus a 30-year test (economic rotation age) plus five years to complete the breeding in a greenhouse (Mike Greenwood, pers. comm.).

Under these assumptions a $r_{J,M}$ of only .20 is required to make E = 1. At first glance this low value looks encouraging in that repeated experimentation should almost certainly result in discovery of some early trait measured in the right environment which would result in a correlation at least as large as .20. However, there are practical problems that will deter the establishment of the true genetic correlation between the "early" and "mature" test situations not the least of which is the fact that well-designed genetic tests of an economically mature age are almost impossible to find. Very often, rank performance of families in a greenhouse or nursery are compared, instead, with the ranks of the same families tested under field circumstances but measured at ages much younger than economic maturity. Such comparisons are still useful if field tested families are at an age suitable for selection, as determined by other evidence. As mentioned earlier, selection is often conducted in 5 to 10-year-old genetic tests. Now, how efficient is an "early test" as compared with, say, an 8-year-old test which is assumed to be optimum for field selection? Under the above assumptions and regarding 8 years as the "mature" selection age, a much larger $r_{J,M} = .54$ is needed for E = 1.

RESEARCH PROBLEMS

Sampling

Correlation analysis is the most commonly employed research into the effectiveness of "early testing", i.e., family performance in the "early test" is correlated with older field performance. While older field tests provide an excellent opportunity to determine the value of "early tests", the correlation approach is fraught with difficulties. A study designed to determine the true genetic correlation between family performances in two circumstances is much more difficult than designing a study simply to determine whether or not there are among family differences for a certain trait because of the inherent problems associated with sampling in a bivariate population.

The correlations plotted in Figure 1 were generated by independent samples from a population with a between groups variance (σ_F^2) of .07 and a within group variance (σ_W^2) of .93. If the groups are families then the ratio $\frac{\sigma_F^2}{\sigma_F^2 \sigma_W^2} = .07.$ would represent a heritability of .14 for full-sib families or .28 for half-sib families or somewhere in between for open-pollinated families (assuming no dominace variance or epistasis), all realistic heritability values for a genetic test. A correlation was generated with the computer as follows:

1. A set of random values estimating a variance of .07 and mean of zero were generated. These represent a population of "family" means from which two independent samples of "individuals" within "families" were generated.

2. "Individuals" within each "family" were generated by drawing random numbers from a population with a variance of .93 and a mean determined by the "family" value obtained in (1). Two sets of "individuals" within "families" were drawn.

3. A rank correlation between "family" means as estimated from the two independent sets of "individuals" within families was calculated. Each solid point (▲ or ●) represents the average of ten such correlations. The open points (△ or ○) are the highest and lowest of the ten correlations.

Even though the underlying correlation is r = 1.0, none of the sample correlations reached that level and most were well below. The correlations increase, and the range decreases dramatically as the number of "individuals" within "families" increases. The correlations based on 10 rather than 25 "families" were generally lower and their range wider. With 150 "families" and 200 "individuals" per "family" the mean correlation is r = .92 with a range of .90 to .94.

If these correlations are realistic in terms of what could be expected from "early testing" studies, then the sample sizes (numbers of families and individuals within families) are extremely critical in detecting the true relationship between "early testing" and field testing. A study based on too few families and individuals could yield almost any correlation.

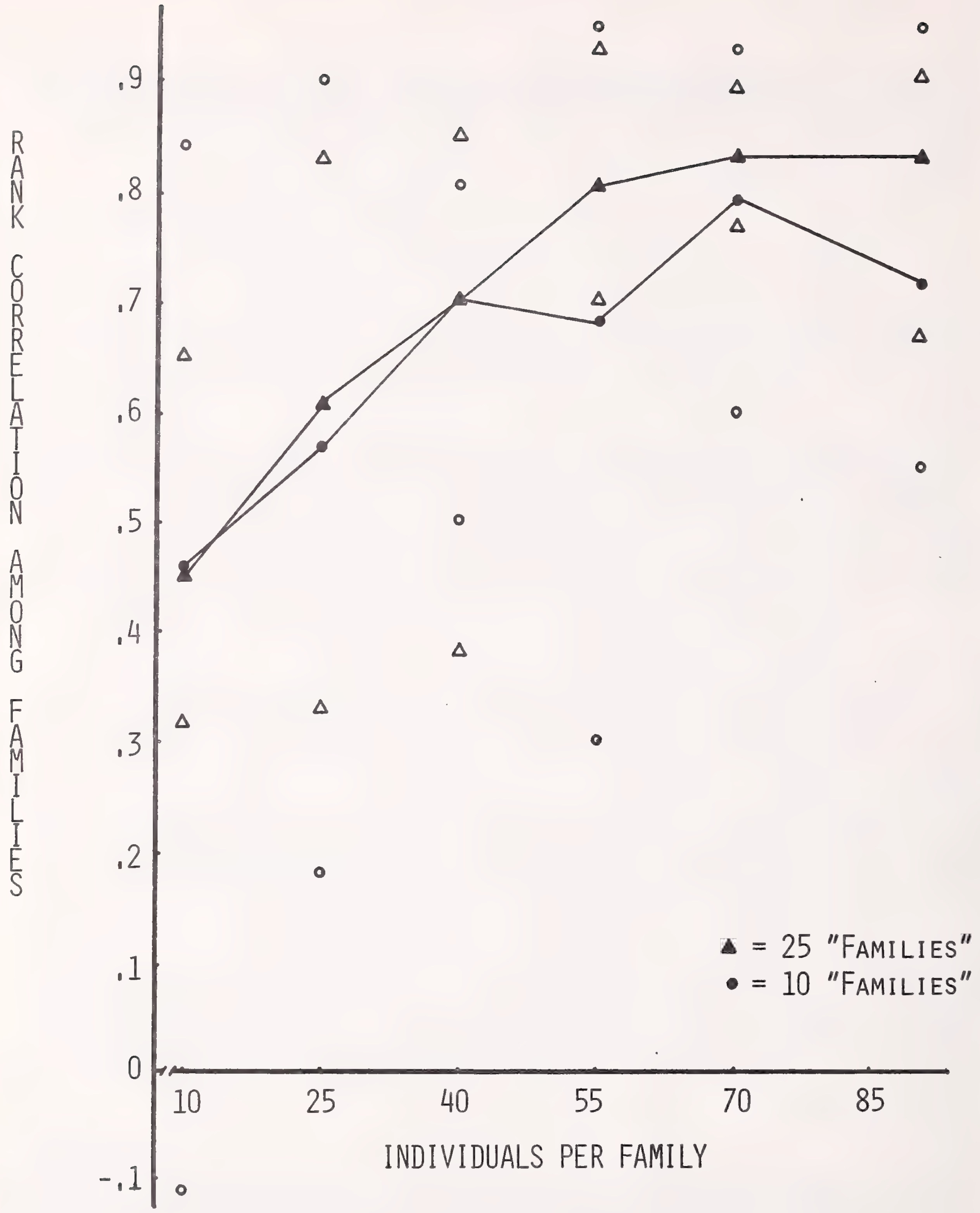

Figure 1. Computer-simulated rank correlation among "family" means when two independent sets of individuals are used to calculate the "family" mean. The estimated variances were .07 and .93 for among and within "family" variances, respectively. Solid points represent a mean of ten runs while the open points represent the high and low values of ten runs.

If one samples from a population whose underlying correlation is less than r = 1.0 then the problems associated with sampling error are even worse. In fact, it may be virtually impossible to detect and characterize some low to moderate genetic correlations between the "early test" and the field test due to biological limitations, even though the correlation may be of sufficient magnitude to be useful in an operational tree improvement program. Perhaps this is one reason that, after decades of research in this area, there is no general consensus on whether or not "early testing" can work.

The sampling problems associated with correlation analysis in "early testing" must be understood by the researcher. The important lesson here is that compromises in experiment size may lead to inconclusive or misleading conclusions. There is an especially strong temptation to make compromises in sample size when measuring certain physiological or otherwise complicated processes in the "early test" because of the time and cost associated with measurement.

Miller (1982) and Waxler and van Buijtenen (1981) avoided some of the sampling problems associated with estimating a correlation between the "early test" and field test by testing extremes. They used the same set of five fast- and five slow-growing families in 10- to 20-year-old field tests and simply tried to classify the families properly based on greenhouse testing. In both studies, mean total dry weight of families in several environments correctly classified four of five families, i.e. four of the top 5 greenhouse families were also classified as fast-growing in field tests.

Seed Effects

Traits such as seed weight and germination rate may influence very early performance of families. If these effects are short-lived the result may be to confound "early test" family ranks and thus reduce the correlation with older field performance which may not be related to seed effects. Lambeth et al. (1982) showed that seed weight, speed of germinatión and average number of cotyledons were related to greenhouse and growth chamber performance of Douglas-fir full-sib families but not with 6th-year height in three field tests. Waxler and van Buijtenen (1981) report similar findings for loblolly pine. In the Douglas-fir study, family AA X BB had the heaviest seed, quickest germination rate and the largest number of cotyledons per tree. It also ranked highest in mean total dry weight in 12 phytotron environments. Since this family did not perform well (rank 11th of 16 families) after six years in the field, it appears to be an outlier when "early test" family ranks are plotted against field ranks (Figure 2). When this family is dropped, the correlation between the early test and field results increases from r = .56* to r = .67**. An inspection of annual field measurements revealed that this family was also top-ranked in the first few years immediately following planting but its performance rank fell in subsequent years.

The influences of seed on "early test" performance need to be better understood. Perhaps one way to get beyond seed influences would be to grow larger plants in a two-year, nursery or greenhouse test.

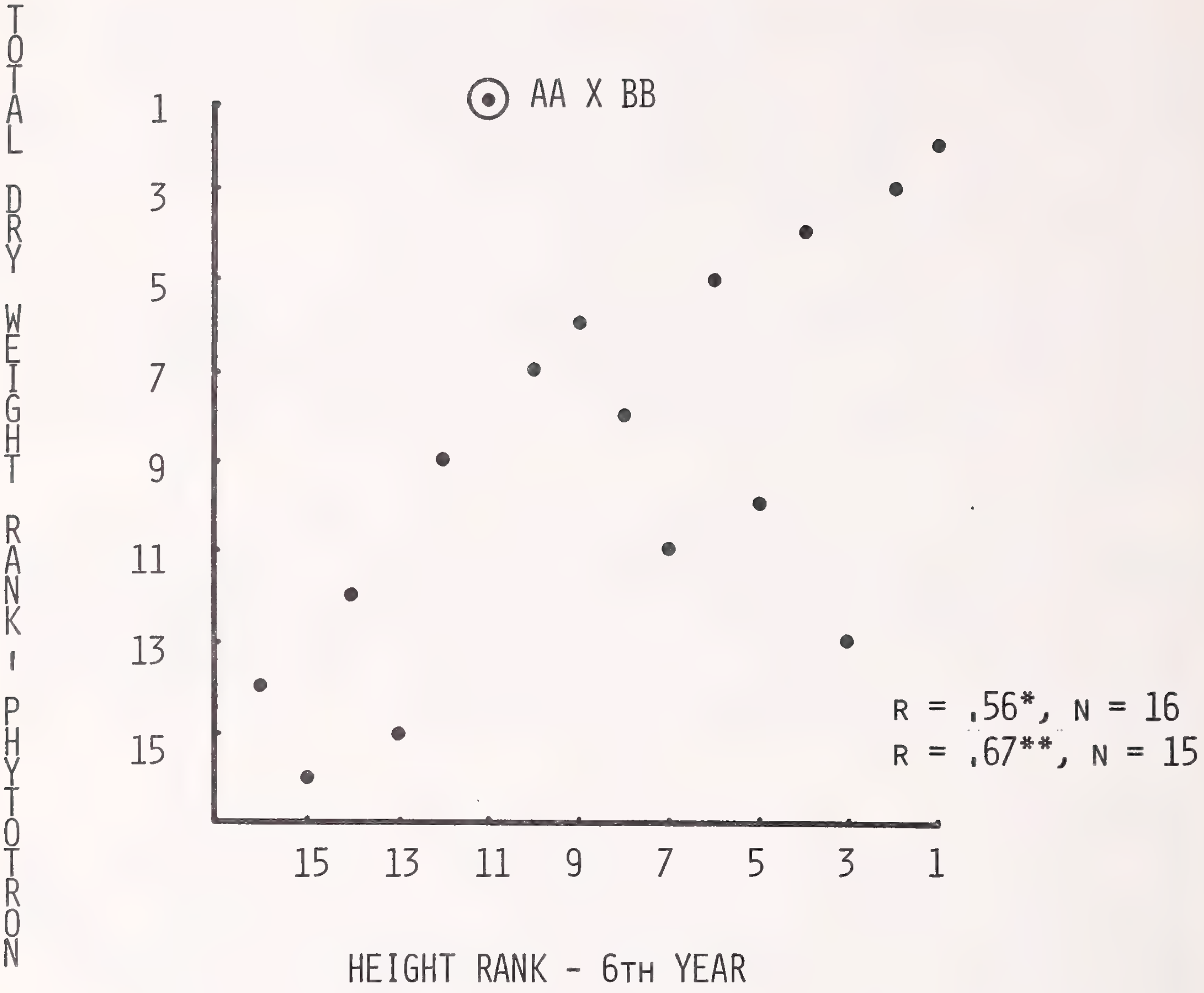

Figure 2. Phytotron versus sixth-year field height rank of Douglas-fir full-sib families (1 = Best, 16 = Worst). Total dry weight is the mean of the family in all 12 phytotron environments. The circled point represents the best family in the phytotron (presumably due to seed effects) which ranked only 11th of 16 in the field. Correlations shown are for all points (n = 16) and after deletion of family AA X BB (n = 15).

CHOICE OF TRAIT IMPORTANT

Recent studies (Miller 1982, Lambeth *et al*. 1982, Duke and Lambeth 1982, Waxler and van Buijtenen 1981) have suggested that family shoot or total dry weight may be better predictors of field performance than total height or, especially, height growth increment when dealing with small trees of the size usually encountered in greenhouse "early tests". The tendency of conifers to periodically halt height growth and set a resting bud, even when the environment is held constant, contributes to the inaccuracy of height increment as a predictor; i.e., some families are resting while others are growing. Nonetheless, when a plant has a resting bud it may still grow considerably in biomass if the environment is favorable. Over a period of a few months in the greenhouse, total height can be an adequate predictor of family field performance though it is usually still not as reliable as total dry weight.

There has been some hope that measurement of certain physiological processes that contribute to early size may be better indicators of later growth potential than early size itself. To my knowledge this is yet an unproven hypothesis.

GENOTYPE - ENVIRONMENT INTERACTION

Whether or not genotype-environment interactions are important to success in "early testing" is still unresovled. If they exist then the degree of correlation with field results will depend strongly on the choice of "early test" environment. The four studies mentioned in the preceding section were all multiple-environment experiments and all resulted in the conclusion that there were no serious genotype-environment interactions. Family ranks were reasonably consistent from one greenhouse environment to another. Family rank changes did occur but they were not beyond the realm of what might be attributed to sampling error.

Lambeth *et al*. (1982) found that the traits which showed the best correlation between family ranks in the phytotron and 6th-year field height also showed the least evidence of genotype-environment interaction. In an analysis of 12 phytotron environments (varying fertility, moisture, lighting, temperature and relative humidity), total dry weight showed almost no variation attributable to full-sib family-by-environment interaction. There were 16 families and 25 trees per family in each environment. The family rank correlations with 6th year field height on three sites varied considerably (Table 1) by environment from $r = .07$ to $r = .75^{**}$; a result consistent with the variance of sampled correlations in Figure 1. Overall, the correlations were certainly encouraging. By contrast, height increment showed considerable variance due to genotype-environment interaction and poor correlation with field results (Table 1).

Table 1.--Correlations between family ranks for total dry weight and height increment in 12 phytotron environments and 6th-year height in field tests (Lambeth et al., 1982).

	Environment											
	1	2	3	4	5	6	7	8	9	10	11	12
Total Dry Wt.	.53*	.55*	.49*	.59*	.59*	.41	.75*	.61*	.07	.14	.41	.50*
Height Increment	.12	.64*	.00	.37	-.54*	-.13	.02	-.18	-.14	.04	-.14	-.14

Until genotype-environment interactions are better understood it is probably best to conduct multiple - rather than single-environment "early tests". A single-environment test may yield poor correlation with field results if it so happens that the choice of environment results in unusual ranking of families.

One approach currently being studied is to conduct a multiple-environment "early test" and screen families not only for overall performance rank but for stability of rank as well. The circled points in Figure 3 represent open-pollinated families with poor rank stability in a greenhouse test of loblolly pine in three environments (Duke and Lambeth, 1982). These tend to lie to the outside of a significant regression with a correlation of r = .51* with 8th-year field volume. When these points are deleted, the correlation improves to r = .74**. Thus the probability of making the correct choice of families in the "early test" improves if families with unstable ranks are first screened from consideration. This hypothesis holds up for three other data sets and is currently under further investigation. Whether or not the rank instability of these families is due to experimental error or genetic response to changing environments is unknown but, whatever the cause, if the geneticist does not have confidence in the overall rank of a family in the "early test", then that family would also be a poor choice for varying field environments that would certainly be encountered.

ADAPTATION

Development of "early testing" methods requires concentration on other traits as well as growth rate, especially in areas where the environment requires populations with good resistance to drought, frost, snow bend or disease. Selection for growth rate alone in an artificial environment could lead to the development of populations poorly adapted to the rigors of field environments.

Fortunately, many adaptation problems show up early in stand development. Mortality due to moisture stress occurs primarily in the two years after planting in most areas where loblolly pine is planted. "Early tests" in stress beds are successful at identifying drought resistance seed sources and families (van Buijten 1966, Lambeth and Burris 1982). Testing of seed sources for use

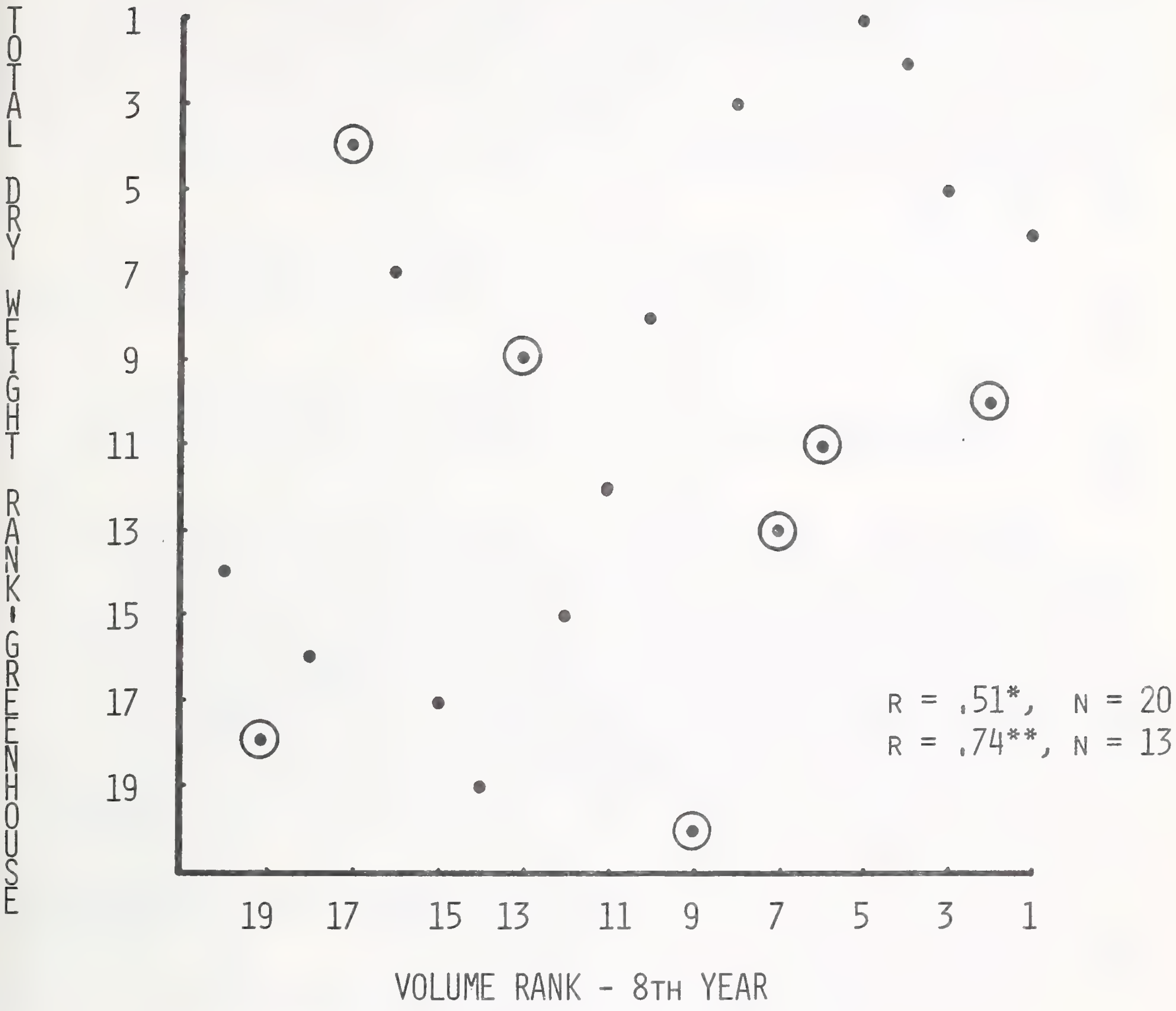

Figure 3. Greenhouse versus eighth-year field volume rank of open-pollinated families of loblolly pine (1 = Best, 20 = Worst). Circled points are families with poor rank stability across the three greenhouse environments. Correlations shown are for all points (n = 20) and after deletion of circled points (n = 13).

at the northwestern fringe of the natural loblolly pine range in Arkansas and Oklahoma have shown good agreement between growth rate, as measured in the greenhouse, and survivability, as measured in a sandy nursery soil, are good measures of field performance (Figure 4). The large differences in growth rate among seed sources, are very often exhibited at very young ages, and persist through to economic maturity (Namkoong et al. 1972, Namkoong and Conkle 1976, Nanson 1974). "Early testing" for growth has been more successful for provenances than for families within provenances. A most likely explanation is that differences among provenances are usually large and therefore easier to detect experimentally.

Frost damage also plagues seedlings more often than large trees. The tendency of seedlings to break bud early and grow late into the season makes them more susceptible. "Early tests" of frost resistance should be successful under the right testing circumstances.

As more data comes in, confidence in the ability to identify slash and loblolly pine families with good rust resistance for field plantings through artificial inoculation procedures in the greenhouse grows (Miller and Powers, 1983).

Direct assessment of some traits such as straightness and resistance to bending by snow and ice will be difficult in an "early test" but indirect selection for these qualities may be possible through measurement of other traits such as specific gravity which tends to have high correlation between juvenile and mature wood (McKinley et al. 1982, Talbert et al. 1983). Direct evidence that high specific gravity is related to straightness (Dietrichson 1964, McKinley et al. 1982) is also supported by the fact that there is a strong correlation which shows that trees with a high Modulus of Elasticity have low specific gravity (Pearson and Gilmore 1980). It seems logical that high elasticity would result in the tendency to crooked growth due to natural forces that bend the tree but more direct study of the relationship between specific gravity and straightness is needed.

In summary, adaptation traits seem to lend themselves better to "early testing" than does growth rate, but the methodologies have not been determined for all traits of concern.

WHERE ARE WE AND WHERE DO WE GO FROM HERE?

Research

Obviously, more work is needed to determine the value of "early testing" for growth rate. Studies examining the relationship between greenhouse or nursery performance versus longer term field performance are quick and valuable. However, more efforts of the type where "early" family selections are made and then carried through to field tests will provide the most conclusive evidence of the "utility or futility" of "early testing". A study of this type by Robinson et al. (1983) showed that "early" screening of families for growth rate resulted in a 28% 5th-year volume gain in follow-up field tests. Twenty-seven of 28 select families outperformed their check lot.

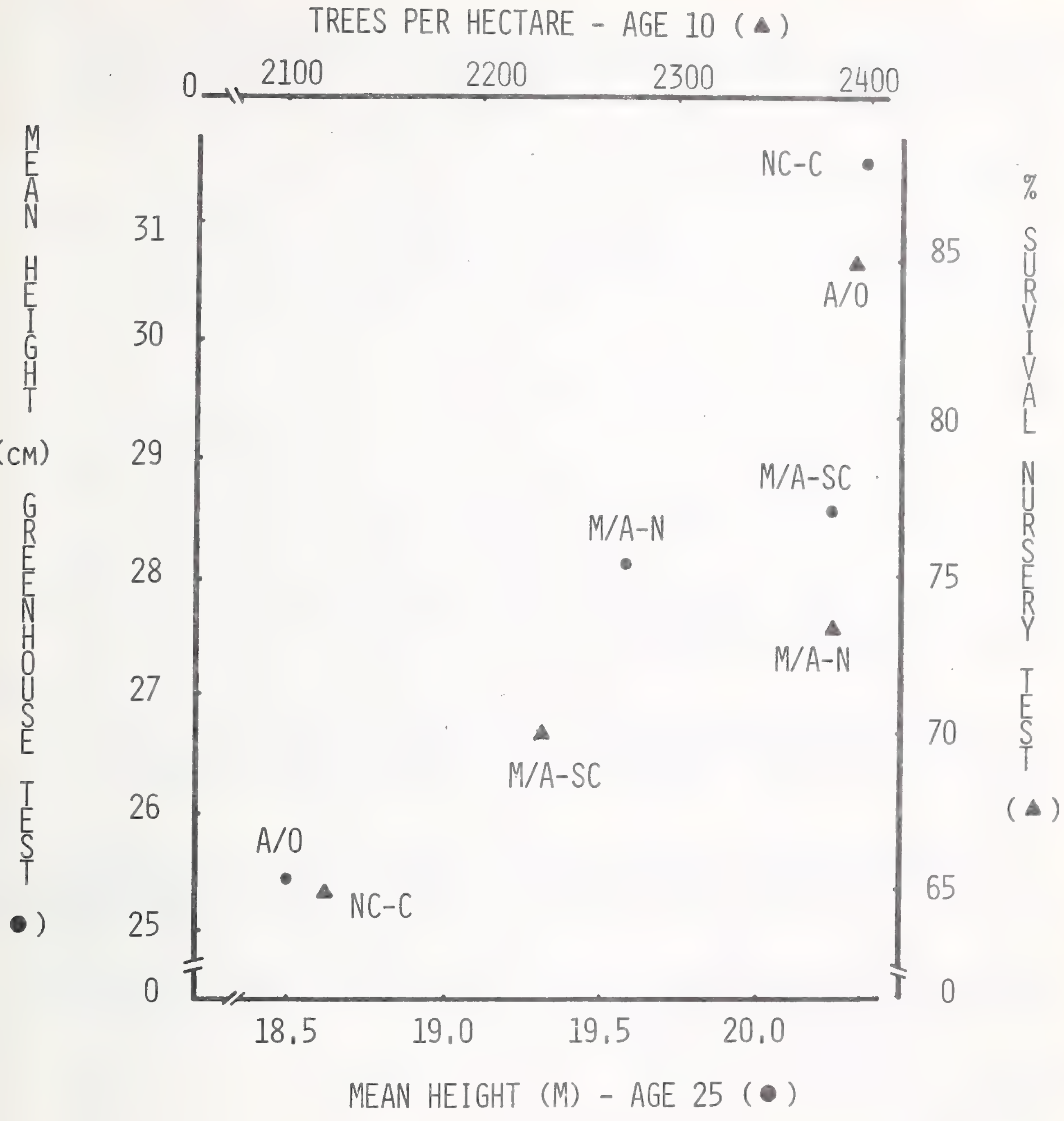

Figure 4. Height and survival assessments of loblolly pine seed sources in greenhouse and nursery tests versus a long-term field test (Wells and Lambeth, 1983).

NCC = North Carolina Coast
A/O = Arkansas and Oklahoma
M/A-N = Northern Mississippi and Alabama
M/A-SC = South Central Mississippi and Alabama

Enough positive evidence from "early testing" research to date warrants the establishment of experimental populations which are cycled through generations as rapidly as possible by employing "early testing" and accelerated breeding. A six- to seven-year generation cycle should be possible with existing technology. These could be specialized populations where selection for a single trait might yield varieties with high specific gravity, good fusiform rust resistance, drought resistance or high volume yield.

In other populations, selection could be carried out for several traits in each generation. One approach would be to test for different traits under different types of "early tests". "Early tests" seem to work best when specifically designed to accentuate the expression of the trait of concern, e.g., fusiform rust resistance through greenhouse inoculation and drought resistance by inducing mortality in stress beds. A proposed scheme for accelerated generation cycling with primary emphasis on growth rate may involve intense selection on size at the family and individual levels combined with low level culling of families for adaptability traits. To ensure that the population does not move away from adaptation to field environments, families could be culled for poor survivability and the nursery test for growth rate occurs in the same geographic area where the material would be commercially planted to ensure exposure to local winter conditions. Poor rust resistance and low specific gravity families could also be screened out through culling levels independent of other traits. Culling on secondary characteristics is conducted to ensure that the population does not lose ground in these traits for whatever reason; e.g., genetic drift or negative genetic correlations between growth and other traits.

The fact that these accelerated breeding and testing populations would start out as experimental populations would not preclude their operational use if the techniques are successful. These populations should be periodically tested against material from conventional tree improvement programs in long-term field trials.

Forestry needs an effort akin to the oil and protein improvement program in maize at the Illinois Agricultural Experiment Station (Dudley, 1974). Over eighty generations of selection that started with only one variety have produced results far beyond the expectations of those who worked in the program in its infancy and continued gains are being realized. The program started in 1896, before the rediscovery of Mendel's papers, and has had only rare interruptions. Invaluable data regarding responses to various types of artificial selection have been the reward. Undoubtedly, such commitment in forestry would be similarly rewarded.

Applications

Some "early testing" is already in practice. Techniques in "early testing" for drought resistance in loblolly pine that are being used to develop drought hardy strains for use in east Texas (van Buijtenen 1966). Fusiform rust resistance screening in slash pine is also an operational reality. To my knowledge, fusiform rust resistance screening is not presently being used operationally in loblolly pine though such should be the case in the very near future.

It is conceivable that enough data to warrant "early testing" for growth rate will be in within 5 to 10 years. The first attempts may involve alternating generations of "early testing" and longer term field tests until complete confidence in the latter is sufficient.

Research has yielded sufficient evidence to indicate that "early testing" to screen out the very slow growing families from field testing is possible. Rarely would the very worst families in a short-term greenhouse or nursery test perform well in older field tests. This form of "early testing" does not shorten the generation cycle since the long-term field test is still used for final selection. It is purely intended to make the overall testing process more efficient or less expensive.

LITERATURE CITED

Dietrichson, J. 1964. The selection problem and the growth rhythm. Silv. Gen. 13(6):178-184.

Dudley, J. W. (ed.). 1974. Seventy generations of selection for oil and protein in maize. Crop. Sci. Soc. of Amer., Inc. Madison, Wisconsin. 212 pp.

Duke, S. D. and C. C. Lambeth. 1982. Early screening of loblolly pine families in an artificial environment. Weyerhaeuser Tech. Note 050-1204/2. 5 pp.

Falconer, D. S. 1960. Introduction to quantitative genetics. The Ronald Press Co., New York. 365 pp.

Lambeth, C. C. and L. C. Burris. 1983. Arkansas/Oklahoma seed source best overall in 1982 field and nursery survival tests. Weyerhaeuser Tech. Note 050-1204/4. 5 pp.

Lambeth, C. C., R. W. Stonecypher and B. J. Zobel. 1982. Early testing of Douglas-fir in phytotron environments - the effect of selection trait and genotype-environment interaction. Proc. 7th North Amer. For. Bio. Workshop, Lexington, Kentucky. Pp. 137-148.

Lee, C. and J. O. Rawlings. 1982. Design of experiments in growth chambers - uniformity trials in the North Carolina State University phytotron. Crop Sci. 22:551-558.

McKinley, C. R., W. J. Lowe and J. P. van Buijtenen. 1982. Genetic improvement of wood specific gravity in loblolly pine (*Pinus taeda* L.) and its relation to other traits. Proc. TAPPI Res. and Dev. Div. Conf. Pp. 153-158.

Miller, D. E. 1982. Early selection of loblolly pine based on genotype x fertilizer interaction of seedlings. M.S. Thesis, Dept. For, Texas A&M Univ. 91 pp.

Miller, T. and H. R. Powers, Jr. 1983. Fusiform rust resistance in loblolly pine. Artificial inoculation versus field performance. Plant Disease 67:33-34.

Namkoong, G. and M. T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. For. Sci. 22(1):2-12.

Namkoong, G., R. H. Usaris and R. R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas-fir. Theor. and Appl. Gen. 42:151-159.

Nanson, A. 1974. Tests precoces de provenances d'Epicea commun. Trav. Stat. Rech. Eaux et For. Groenendaal, Ser. E. No. 6, 38 pp.

Pearson, R. G. and R. C. Gilmore. 1980. Effect of fast growth rate on the mechanical properties of loblolly pine. For. Prod. J. 30(5):47-54.

Robinson, J. F., J. P. van Buijtenen and E. M. Long. 1983. Very early traits can be used to select for later volume of loblolly pine. (*In* press South. J. Appl. For.).

Talbert, J. T., J. B. Jett and R. L. Bryant. 1983. Inheritance of wood specific gravity in an unimproved loblolly pine population: 20 years of results. Silvae Genetica (*In* Press).

van Buijtenen, J. P. 1966. Testing loblolly pines for drought resistance. Texas For. Ser. Tech. Rep. 13. 15 pp.

Waxler, M. S. and J. P. van Buijtenen. 1981. Early genetic evaluation of loblolly pine. Can. J. For. Res. 11:351-355.

Wells, O. O. and C. C. Lambeth. 1983. Loblolly pine provenance test in southern Arkansas - 25th-year results. South. J. Appl. For. 7(2):71-75.

BIOCHEMICAL METHODS FOR ACCELERATING PROGRESS IN TREE IMPROVEMENT

James W. Hanover[1]

Abstract.--The theory and practice of physiological genetic approaches to solving problems in tree improvement are discussed. The advantages of using biochemical techniques are summarized and a range of applications is described. These include measurements of genetic variability, degree of relatedness between populations, species and hybrids, breeding structure of populations, inbreeding in seed orchards, and increasing selection efficiency. Biochemicals are also proving to be useful in shortening tree breeding cycles. Some future directions in biochemical breeding of trees are outlined.

Additional keywords: Indirect selection, molecular markers, terpenes, isozymes.

Tree breeders are fortunate in having a considerable amount of natural variation as a basis for selection in most species and traits of commercial importance. On the other hand progress in tree improvement is severely constrained for two major reasons. First, phenotypic selection in the wild or even in plantations is often ineffective (Pitcher 1982) and usually inefficient because narrow sense heritabilities for complex traits are mostly low necessitating long term progeny testing. Second, both generation and rotation intervals in trees are long which, combined with the occurrence of juvenile-mature phase changes, hinder early evaluation of trait expression and accomplishment of advanced generation breeding. These two prime constraints to tree improvement have stimulated interest and research on two possible methods for alleviating them: (1) clonal propagation of improved planting stock (Libby 1977; Hanover and Dickmann 1982; Eliasson 1977; Eriksson and Lundkvist 1981; Armson, *et al*. 1980; Karnosky 1981; Farnum *et al*. 1983) and, (2) techniques for accelerating the process of genotype evaluation, selection, and breeding of superior types.

Biochemical approaches are potentially useful in both of the methods suggested for stimulating more rapid progress in tree improvement (Hanover 1974). My purpose here is to focus on ways in which biochemical techniques may be used by tree breeders to transform potentials for progress into reality. I would emphasize, however, that such techniques must always supplement and enhance but certainly not replace the standard methods of tree improvement with which we are all familiar.

PHYSIOLOGICAL GENETICS OF QUANTITATIVE TRAITS

The quantitative traits that plant breeders are mainly concerned about, such as yield, form, hardiness, and resistance to pests, are usually controlled by many structural and regulatory genes. We refer to such traits as "complex". For convenience, breeders have typically treated such traits as simple or unitary in their research and improvement programs (Malmborn 1967). This practice may be appropriate in the early stages of a breeding program but as genetic gains become more difficult to achieve or perhaps even sooner, we should consider the use of component characters as bases for selection. The elucidation or "dissection" of a quantitative character into its primary components constitutes the physiological genetic approach to plant breeding. Implicit in physiological genetic studies is the enormous range of biochemical constituents and processes found in trees about which we know relatively little (Hanover 1974).

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The physiological genetic approach to breeding for complex traits involves five basic procedures:

1. Identify important physiological, biochemical, morphological, or anatomical components of the complex trait.

2. Screen for genetic variation in the components and genetic correlations with the complex trait.

3. Determine heritability of the components.

4. Incorporate traits into superior genetic background through breeding.

5. Test for performance of new genotypes in appropriate environments.

It should be obvious that only the first step and part of the second are unique to physiological genetics. That is, the identification of important components and determination of their genetic correlations with the complex trait. Otherwise, the procedures are standard practices for breeders. However, application of physiological genetics to tree breeding and even plant breeding in general is virtually non-existant. This is because the concept is relatively new and the identification of components (step 1) is not an easy task but requires a multidisciplinary effort. Fortunately, biochemical studies of forest trees are now receiving considerable attention by geneticists which should contribute to step (1) above for some of our important quantitative traits. There are, however, several areas in which biochemical methods are currently employed to increase effectiveness and efficiency of tree breeding programs. One of these areas is the use of molecular markers and indirect selection (Tanksley 1983; Squillace 1976; Hanover 1974; Kriebel 1980; Bridgen and Hanover 1982).

THEORY AND OBJECTIVES OF INDIRECT SELECTION

The underlying theoretical basis for finding and using biochemical markers to accelerate tree selection and breeding resides in the concept of indirect selection. Indirect selection is simply selection applied to any character other than the one for which improvement is desired (Falconer 1960). By selecting for a "secondary" character "Y" we may make greater progress towards improving primary character "X" through the correlated response of X with Y. Following are some conditions which favor indirect selection:

1. A high genetic correlation exists between the two traits, X and Y.

2. There is less effort or cost in selecting for Y than X directly.

3. Less time is required per generation for improvement of X when selecting for Y.

4. There is a higher precision in measuring Y than X.

5. There is a better correlation between progeny means and parental means for trait Y than trait X.

6. Trait Y has a higher heritability than trait X.

7. A higher selection intensity can be applied to trait Y than to trait X.

8. Trait X can be measured in only one sex, Y in both.

9. Trait Y is a juvenile trait that can be measured earlier in the life cycle than trait X.

Calculation of the expected gains (G_X) or correlated response in trait X by selecting for trait Y is obtained by:

$$G_X = i_Y h_Y r_A \sigma_{AX} \text{ (Falconer 1960)}$$

where, i_Y = selection intensity for Y, S/σ_{PY}

h_Y = square root of the operative heritability of trait Y

r_A = genotypic correlation between X and Y

σ_{AX} = square root of the genetic variance of X

One can compare the relative efficiency of using indirect selection (G_X) instead of direct selection (R_X) by calculating the ratio of expected gains for each method:

$$\frac{G_X}{R_X} = r_A \frac{i_Y h_Y}{i_X h_X}$$

APPLICATIONS OF BIOCHEMICAL METHODS IN TREE IMPROVEMENT

Molecular Markers in Tree Breeding

There are several reasons for emphasizing development of biochemical rather than morphological markers to aid tree breeders (Tanksley 1983):

1. Genotypes of molecular loci can be determined at the whole plant, tissue, and cellular levels. Phenotypes of most morphological markers can only be distinguished at the whole plant level.

2. A relatively large number of naturally occuring alleles can be found at molecular marker loci, compared with morphological loci.

3. Usually, no deleterious effects are associated with allele substitutions for molecular markers in contrast to the case with many morphological markers.

4. Alleles of most molecular markers are codominant, allowing all possible genotypes to be distinguished in any segregating generation. Alleles at morphological marker loci are usually dominant or recessive.

5. Epistatic effects are more prevalent in morphological than in molecular marker loci which limits the number of segregating markers scorable in a generation or population.

Examination of some generalized biosynthetic pathways in trees reveals the kinds of molecular markers that are available to breeders (Fig. 1). These include DNA, proteins, especially isozymes, and a wide range of secondary plant products including terpenes, phenolic substances, acetogens, alkaloids and waxes. Each of these classes of compounds has its own particular advantages and disadvantages for use in tree improvement. Of course, if the objective is to determine cause-effect rather than linkage relationships between chemicals and a quantitative trait,that would dictate which chemicals should be studied. Furthermore, it is not reasonable to search for single chemical markers closely linked to genes governing expression of a complex trait and the likelihood of establishing useful linkages between multiple chemical markers and the polygenes of interest is remote. Therefore, DNA and protein markers will initially be of most value in characterizing the breeding structures of populations and species and for estimating genetic distances between taxons rather than as marker genes for indirect selection of complex traits. Secondary plant products do offer excellent possibilities for practicing indirect selection as well as helping to solve other problems in forest genetics.

Any component character of a complex trait is a potential candidate for use in improving the primary trait by indirect selection. The components may be related to the primary trait either through tight linkage or pleiotropic (cause-effect) gene action. Thus, an array of morphological, anatomical, physiological and biochemical components are being researched by crop scientists for predicting indirect selection response in primary traits such as yield, form, quality, or pest resistance (Larsson 1982; Chen et al. 1982; Hitz et al. 1982; Bhatt et al. 1979; Tanksley 1981). Because tree breeders are vitally concerned with developing methods for early selection and evaluation of progeny performance,research related to indirect selection in trees is beginning to receive more attention (Rudin 1976, 1979; Squillace 1976; Rockwood 1973; Harris and Borden 1982; Bridgen and Hanover 1982; Weissenberg 1976; Hanover 1975, 1980). As already indicated earlier we are concerned here only with the application of molecular or biochemical systems analysis in tree improvement.

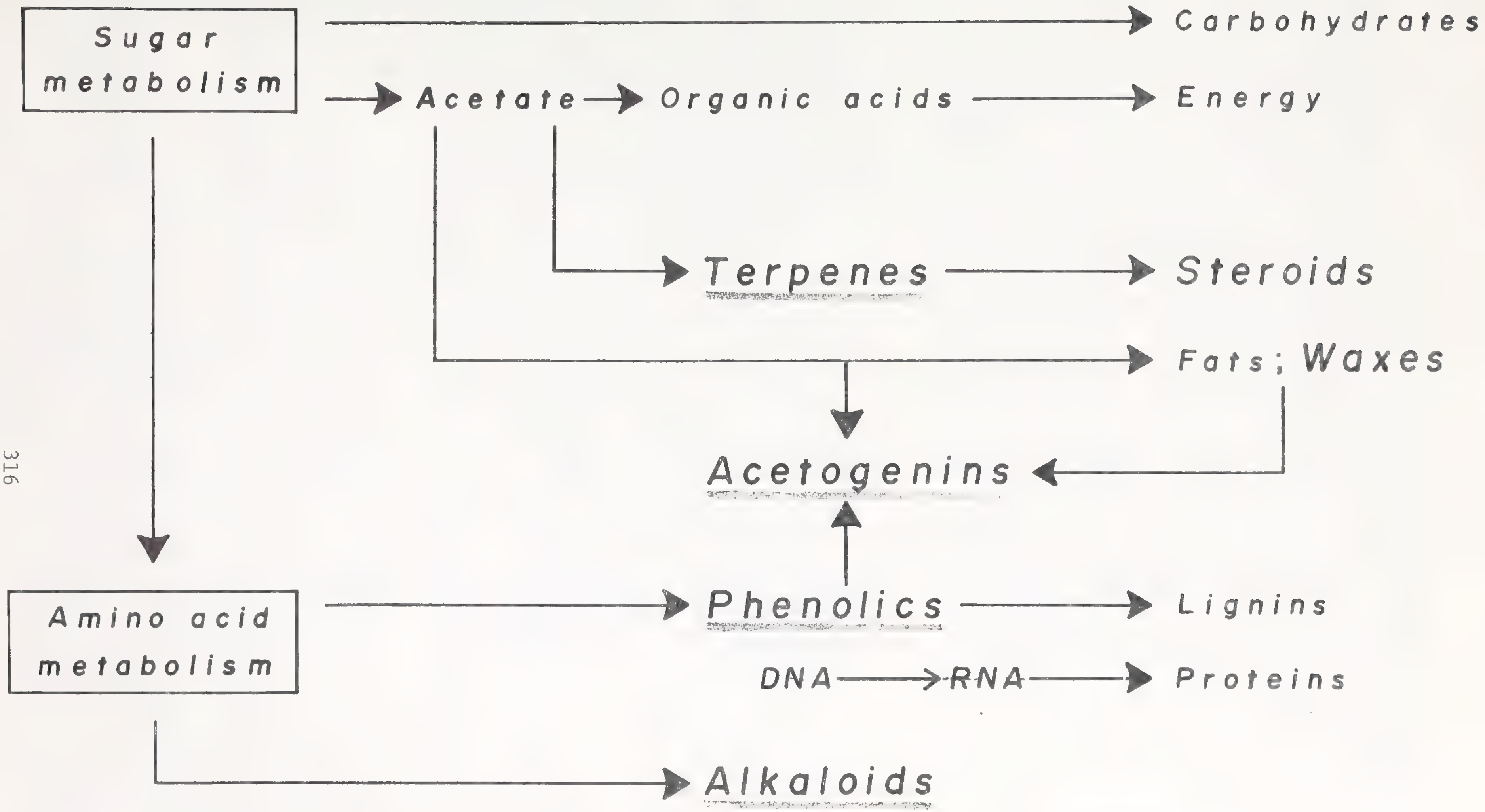

Fig. 1. Generalized biosynthetic pathways showing primary and secondary (lightly underlined) chemical classes which may be used as molecular markers for indirect selection.

Applications to Selection and Breeding

Biochemical markers are of direct benefit to tree breeders when they serve as correlated traits for practicing indirect selection. One of the best examples of this use is in tomato where Rick and Robes (1974) discovered a remarkably tight linkage between an acid phosphatase locus (Aps-1) and the gene for resistance to root-knot nematodes (Mi) (Medina-Filho 1960). Seed companies now use this marker to: (1) identify resistant plants at a much earlier stage, (2) distinguish resistant and susceptible plants with ease and accuracy, and (3) distinguish between homozygous and heterozygous plants without progeny testing for nematode susceptibility (Rick 1982).

In spite of this elegant example in tomato of how indirect selection may be accomplished with molecular markers, our chances of finding such simple systems in other plants and trees are slight. As mentioned earlier this is because most of our important traits are polygenic rather than monogenic so identification of multiple markers would be required. Nevertheless, the principle of indirect selection using molecular markers is sound and I would like to suggest a strategy for developing and employing indirect selection for quantitative traits in trees. The proposed strategy is summarized in Figure 2.

In searching for either or both linkage and pleiotropic relationships between important quantitative traits and chemicals literally thousands of chemicals can be rapidly and accurately screened. This is due to the availability of powerful analytical tools such as gas and liquid chromatography and electrophoresis. Combined with computerized multivariate analytical techniques relationships (correlations) between chemicals and complex traits can be established. Those correlations that are consistent and meet the other requirements outlined earlier for secondary traits can be used in multivariate analyses such as discriminate or factor analysis to construct an index. Index selection comprising a series of molecular markers would then be the basis for obtaining more rapid improvement in the primary trait of interest. Although no data are available to illustrate the utility of molecular marker indices for selection, we are working towards this end with terpenes, aromatic compounds, and isozymes in the spruces, firs and pines.

Once molecular marker index selection techniques are developed they should be important adjuncts to all aspects of selection and advanced generation breeding for metric characters.

Applications to Other Problems in Forest Genetics

Chemical markers are now widely used in solving problems or providing basic information for tree breeders. Time will not allow any detailed consideration of these uses but I would like to summarize them to briefly indicate the principles underlying each use. Table 1 lists the major applications for chemical markers and some selected examples from the literature.

From this admittedly incomplete summary it is apparent that interest in chemical markers in trees is high. There are innumerable examples of published and unpublished research on chemical markers that are inconclusive or incomplete at this time in terms of providing data of specific practical use. However, as biochemical methods continue to be explored, expanded and refined, we can expect substantial benefits to forest genetics in the near future from both the basic and applied aspects.

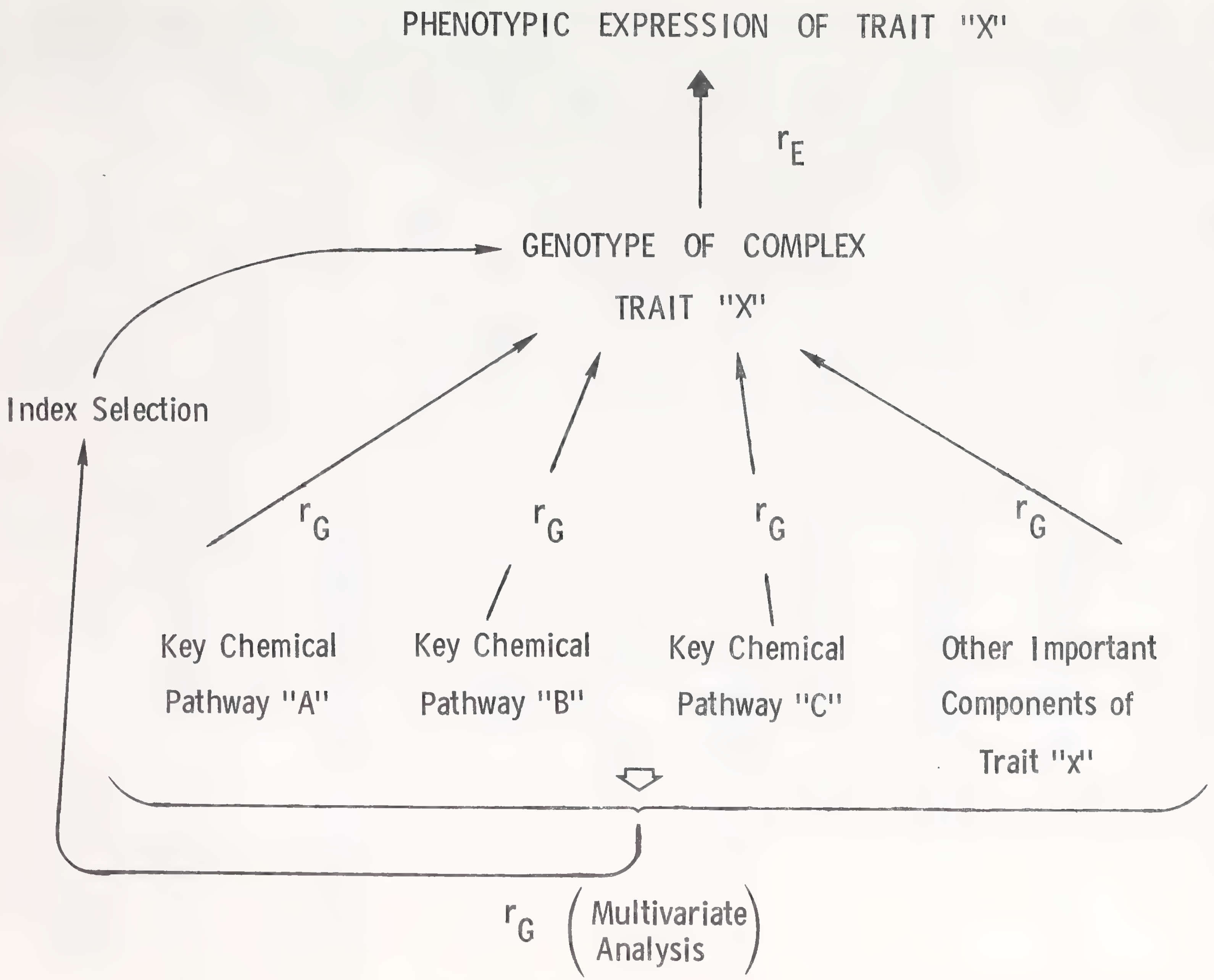

Fig. 2. Application of biochemical and morphological markers in combination with multivariate analysis and index selection for improvement of a complex trait.

Table 1. Applications of chemical markers to forest genetics problems.

Application	Example
Early selection of a chemical trait which itself is of primary interest	Sap sugar in sugar maple (Kriebel 1960) Oleoresin composition in slash pine (Squillace 1977) Leaf surface wax for foliage color in blue spruce (Hanover 1975)
Assessment of population variability	Isoyzmes (Conkle 1972; Guries and Ledig 1977, 1982; Lundkvist and Rudin 1977; etc.) Terpenes (Hanover 1974)
Assessment of geographic variability	Terpenes (Tobolski and Hanover 1971; Squillace and Wells 1981; Wilkinson and Hanover 1972; Bernard-Dagan _et al_. 1971; Gausel and Squillace 1976) Isozymes (Weber and Stettler 1981; Wheeler and Guries 1982)
Identification of clones, seed sources, and natural or artificial hybrids; seed identification	Terpenes (Rottink and Hanover 1972; Hanover and Wilkinson 1969; Bongarten and Hanover 1982; Squillace _et al_. 1980) Phenolics (Hoff 1968; Hanover and Wilkinson 1970: Isozymes (Bergmann 1972) DNA (Miksche and Hotta 1977)
Estimation of outcrossing and inbreeding rates in natural populations and seed orchards	Terpenes (Squillace and Kraus 1963) Isozymes (Adams and Joly 1980; Rudin and Lindgren 1977; Shaw and Allard 1982; Mitton _et al_, 1977; Adams 1981; Muller 1977)
Measurement of genetic relatedness among species, races and individuals; speciation	DNR, RNA (Kriebel 1982; Miksche and Hotta 1973) Terpenes (Squillace 1982; Hanover 1975) Isozymes (Copes and Beckwith 1977)
Identification of haploid-derived plants from anther culture and of parasexual hybrids	None
Indirect selection using molecular markers correlated with a primary trait	Terpenes (Rockwood 1973, 1974; Bridgen and Hanover 1982; Weissenberg 1973, 1976; Hanover and Furniss 1966) Isozymes (Ryu 1982)

LITERATURE CITED

Adams, W.T. 1981. Applying isozyme analyses in tree breeding programs. U.S.D.A., Forest Service Gen. Tech. Rep. PSW-48, p. 60-64.

Adams, W.T. and R.J. Joly. 1980. Allozyme studies in loblolly pine seed orchards: Clonal variation and frequency of progeny due to self-fertilization. Silvae Genetica 29:1-4.

Armson, K.A., M. Fung, W.R. Bunting. 1980. Operational rooting of black spruce cuttings. J. Forestry 78:341-343.

Bermann, Fritz. 1972. Experiments on possibilities for genetic certification of forest seed. IN Proc., IUFRO and SABRO Joint Meeting, Tokyo, Japan. A-6(V):1-5.

Bernard-Dagan, C., C. Fillon, G. Pauly, Ph. Baradat, and G. Illy. 1971. Les terpenes du Pin maritime: aspects biologiques et genetiques. I. Variabilite de la composition monoterpenique dans individu, entre individus et entre provenances. Ann. Sci. Forest. 28:223-258.

Bhatt, K.C., P.P. Vaishnav, Y.D. Singh and J.J. Chinoy. 1979. Nitrate reductase activity: a biochemical criterion of hybrid vigour in Sorghum bicolor (L.) Moench. Ann. Bot. 44:495-502.

Bongarten, B. and J.W. Hanover. 1982. Hybridization among white, red, and blue spruces and the white x blue spruce hybrid. Forest Science 28:129-134.

Bridgen, M.R. and J.W. Hanover. 1982. Indirect selection for pest resistance using terpenoid compounds. IN: Heybroek, H.M., B.R. Stephan, & K. von Weissenberg (Eds). Resistance to diseases and pests in forest trees. p. 161-168. Pudoc, Wageningen.

Chen, Hwei-Hwang, Zheng-Yan Shen, and P.H. Li. 1982. Adaptability of crop plants to high temperature stress. Crop Sci. 22:719-725.

Conkle, M. Thompson. 1972. Analyzing genetic diversity in conifers -- isozyme resolution by starch gel electrophoresis. U.S.D.A. Forest Service Res. Note PSW 264, 5 p.

Copes, D.L. and R.C. Beckwith. 1977. Isoenzyme identification of Picea glauca, P. sitchensis, and P. lutzii populations. Bot. Gaz. 134:512-521.

Eliasson, Lennart (Ed.) 1977. Vegetative propagation of forest trees - physiology and practice. Proc. Symposium in Uppsala, Sweden, Feb. 16-17, 1977, Swedish University of Agricultural Sciences. 159 pp.

Eriksson, Gösta and Kenneth Lundkvist (Eds.). 1981. Symposium on clonal forestry, Uppsala, Sweden. April 8-9, 1981. Swedish University of Agricultural Sciences, 131 pp.

Falconer, D.S. 1960. Introduction to quantitative genetics. Ronald Press, N.Y. 365 pp.

Farnum, Peter, Roger Timmis, and J.L. Kulp. Biotechnology of forest yield. Science 219:694-702.

Gansel, R. and A.E. Squillace. 1976. Geographic variation of monoterpenes in cortical oleoresin of slash pine. Silvae Genet. 25:150-154.

Guries, R.P. and F.T. Ledig. 1977. Analysis of population structure from allozyme frequencies. IN: Proc. 14th So. Forest Tree Improv. Conf., Gainesville, Fla. p. 246-253.

Guries, R.P. and F.T. Ledig. 1982. Genetic diversity and population structure in pitch pine (Pinus rigida Mill). Evolution 36:387-402.

Hanover, J.W. 1974. Biochemical analysis of tree speciation. IN: Proc. Third North Amer. Forest Biol. Workshop. Fort Collins, Co. pp. 106-131.

Hanover, J.W. 1975. Comparative physiology of eastern and western white pines: oleoresin composition and visiosity. For. Sci. 21:214-221.

Hanover, J.W. 1975. Genetics of blue spruce. U.S.D.A. Forest Service Res. Paper WO-28, 12 p.

Hanover, J.W. 1975. Physiology of tree resistance to insects. Ann. Rev. Entomol. 20:75-95.

Hanover, J.W. 1980. Breeding forest trees resistant to insects. IN: Maxwell F.G. and P.R. Jennings (Eds.) Breeding plants resistant to insects p. 486-511. Wiley-Interscience, N.Y. 683 p.

Hanover, J.W. and D.I. Dickmann. 1982. Systems for production of improved stock for intensive culture. Proc. 7th North Amer. Forest Biol. Workshop, Lexington, Ky.

Hanover, J.W. and M.M. Furniss. 1966. Monoterpene concentration in Douglas-fir in relation to geographic location and resistance to attack by the Douglas-fir beetle. U.S.D.A., Forest Service Res. Paper NC-6, p. 23-28.

Hanover, J.W. and R.C. Wilkinson. 1969. A new hybrid between blue spruce and white spruce. Can. J. Bot. 47:1693-1700.

Hanover, J.W. and R.C. Wilkinson. 1970. Chemical evidence for introgressive hybridization in Picea. Silvae Genetica 19:17-22.

Hitz, W.D., J.A.R. Ladyman, and A.D. Hanson. 1982. Betaine synthesis and accumulation in barley during field water stress. Crop. Sci. 22:47-54,

Hoff, R.J. 1968. Chemical verification of the hybrid of Pinus monticola and Pinus flexibis. Forest Sci. 14:119-121.

Karnosky, David F. 1981. Potential for forest tree improvement via tissue culture. Bio. Science 31:114-120.

Kriebel, Howard B. 1960. Selection and testing for sugar yield in *Acer saccharum* L. Proc. Fifth World Forestry Congress, Seattle, WA.

Kriebel, Howard B. 1980. Research approaches to forest genetics at the DNA level. Proc. Sixth North Amer. Forest Biol. Workshop. Edmonton, Alberta, pp. 49-76.

Larsson, S. 1982. A simple, rapid and non-destructive screening method useful for drought resistance breeding in oats (*Avena sativa* L.) Z. Pflanzenzuchtg. 89:206-211.

Libby, W.J. 1977. Rooted cuttings in production forests. *IN* Proc. 15th Southern Forest Tree Improvement Conference, Gainesville, Florida, p. 13.

Lundkvist, K. and Dag Rudin. 1977. Genetic variation in eleven populations of *Picea abies* as determined by isozyme analysis. Hereditas 85:67-74.

Malmborn, Sven O. 1967. Some aspects of studies of complex characters in the field of genetics. Hereditas 56:109-112.

Medina-Filho, H.P. 1980. Linkage of Aps-1, Mi and other markers on chromosome 6. Rep. Tomato Genetics Coop. 30:26-28.

Miksche, J.P. and Y. Hotta. 1973. DNR base composition and repetitious DNR in several conifers. Chromosoma 41-29-36.

Mitton, J.B., Y.B. Linhart, J.C. Hamrick, and J.S. Beckman. 1977. Observations on the genetic structure and mating system of ponderosa pine in the Colorado front range. Theor. Appl. Genetics 51:5-13.

Muller, G. 1977. Cross-fertilization in a conifer stand inferred from enzyme gene-markers in seeds. Silvae Genetica 26:223-226.

Pitcher, John A. 1982. Phenotype selection and half-sib family performance in black cherry. Forest Sci. 28:251-256.

Rick, C.M. 1982. Isozymes in plant breeding. Calif. Agr. 36:28.

Rick, C.M. and J.F. Fobes. 1974. Association of an allozyme with nematode resistance. Rep. Tomato Genet. Coop. No. 24:25.

Rockwood, Donald L. 1973. Monoterpene - fusiform rust relationships in Loblolly pine. Phytopathology 63:551-553.

Rockwood, D.L. Cortical monoterpenes and fusiform rust resistance relationships in slash pine. Phytopathology 64:976-979.

Rottink, B.A. and J.W. Hanover. 1972. Identification of blue spruce cultivars by analysis of cortical oleoresin monoterpenes. Phytochem. 11:3255-3257.

Rudin, D. 1976. Biochemical genetics and selection - application of isozymes in tree breeding. Proc. IUFRO Meeting on Advanced Generation Breeding, Bordeaux, France. p. 145-164.

Rudin, Dag (Ed.) 1979. Proc. Conf. on Biochemical genetics of forest trees. Swedish Univ. of Agricultural Sci., Umea, Sweden. 201 pp.

Rudin, D. and D. Lindgren. 1977. Isozyme studies in seed orchards. Stud Forest Suec 139:23 p.

Ryu, Jang Bal. 1982. Relations between isozyme variables and height growth of Pinus strobus L. Korean Inst. For. Genet. Res. Rpt. 18, p. 17-27.

Shaw, D.V. and R.W. Allard. 1982. Estimation of outcrossing rates in Douglas-fir using isozyme markers. Theor. Appl. Genet. 62:113-120.

Squillace, A.E. 1976. Biochemical genetics and selection - composition of volatile terpenes. Proc. IUFRO Meeting on Advanced Generation Breeding, Bordeaux, France. pp. 167-178.

Squillace, A.E. 1977. Use of monoterpene composition in forest genetics research with slash pine. Proc. 14th South. For. Tree Improv. Conf.: 227-238.

Squillace, A.E., H.T. Schroeder, and H.T. Battacharyya. 1980. Identification of seed origin of slash pine plantations. Silvae Genetica 29:152-154.

Tanksley, Steven D. 1983. Molecular markers in plant breeding. Plant and Molecular Biology Reporter 1:3-8.

Tanksley, S.D., H. Medina-Filho and C.M. Rick. 1981. The effect of isozyme selection on metric characters in an interspecific backcross of tomato-basis of an early screening procedure. Theor. Appl. Genet. 60:291-296.

Tobolski, J.J. and J.W. Hanover. 1971. Genetic variation in the monoterpenes of Scotch pine. Forest. Sci. 17:293-299.

Weber, J.C. and R.F. Stettler. 1981. Isoenzyme variation among ten populations of Populus trichocarpa Torr. et Gray in the Pacific Northwest. Silvae Genetica 30:82-87.

Weissenberg, Kim von. 1973. Indirect selection for resistance to fusiform rust in loblolly pine. Acta Forestalia Fennica 134:1-46.

Weissenberg, K. von. 1976. Indirect selection for improvement of desired traits. IN: J.P. Miksche (Ed.) Modern methods in forest genetics. Springer-Verlag, 288 p.

Wheeler, N.C. and R.P. Guries. 1982. Population structure, genic diversity, and morphological variation in *Pinus contorta* Dougl. Can. J. For. Res. 12:595-606.

Wilkinson, R.C. and J.W. Hanover. 1972. Geographical variation in the monoterpene composition of red spruce. Phytochem. 11:2007-2010.

POTENTIAL OF *IN VITRO* SCREENING OF LOBLOLLY PINE FOR FUSIFORM RUST RESISTANCE

L. J. Frampton, Jr., H. V. Amerson and R. J. Weir[1]

Abstract.-- Twelve loblolly pine (*Pinus taeda* L.) embryos from each of 24 full-sib families (arranged in a 3 x 8 factorial mating design) were inoculated *in vitro* with *Cronartium quercuum* (Berk.) Miyabe ex Shirae f. sp. *fusiforme* basidiospores. Assessments of two types of responses, incompatible rapid necrosis and the appearance of a dark staining substance, typically at the inoculation point were made. These traits showed high family correlation with field resistance and high family heritabilities and so should be useful in the development of a rapid *in vitro* resistance screening technique.

Additional keywords: Indirect selection, early selection, *Pinus taeda*, *Cronartium quercuum* f. sp. *fusiforme*.

Presently, use of resistant planting stock is the primary and most economically feasible method of managing fusiform rust in plantations of loblolly (*Pinus taeda* L.) and slash (*Pinus elliottii* var. *elliottii* Englem.) pines. In order to reduce the time and effort involved in obtaining resistant ratings from field progeny tests, a greenhouse method of assessing resistance with artificial inoculations is being utilized by the U.S. Forest Service Resistance Screening Center. Select trees are rated based on their progeny performance for six symptom types assessed six months after inoculation (USDA For. Pest Mgt. Rep. #82-1-18, 1982). This method of screening is very useful and may account for 40 to 60 percent of the variation in field resistance (Walkinshaw et al. 1980, Carson 1983). However, development of an *in vitro* method of resistance screening could offer further benefits such as shortening assessment time and effort, better environmental control and the opportunity to better investigate host-pathogen relationships.

Recently, Gray and Amerson (in press, 1983) observed several *in vitro* responses of loblolly pine embryos to infection by *Cronartium quercuum* f. sp. *fusiforme*. Two responses, rapid incompatible necrosis (RN) and the formation of appositions which effectively barricaded the fungus from entering the cell, were regarded as effective resistance responses. The former response, RN, was characterized by the rapid death of host tissue and often resulted in haustorial necrosis. This response showed significant family differences and family rankings corresponding to field resistance rankings for a susceptible, an intermediate and a resistant full-sib family of loblolly pine. However, a family x assessment time and family x inoculum density interaction were present, implying that cultural conditions are crucial when assessing this *in vitro* response.

The purpose of this study is to further investigate the potential of *in vitro* screening of loblolly pine for fusiform rust resistance.

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METHODS

Plant material.--Fifteen embryos from 24 full-sib families arranged in a 3 x 8 factorial mating design were used in this study. These families were part of a 22 parent half-diallel of resistant trees that were established in a series of plantings in high rust hazard areas by the North Carolina State University-Industry Cooperative Tree Improvement Program. Seeds were nicked at the micropylar end and incubated 4 to 5 days at 30°C in 1 percent aqueous hydrogen peroxide, changed daily. Seed coats were then removed and the gametophytes were surface sterilized with 0.8 percent (w/v) sodium hypochlorite solution and rinsed three times with sterile distilled water. Embryos were aseptically excised and their radicles inserted into half-strength Greshoff and Doy medium (Mott and Amerson 1981). Embryos were maintained at $22\pm2^{\circ}C$ in mixed incandescent fluorescent light, 3000-4000 lux, with a 16 hour photoperiod for 13 days.

Inoculum preparation and inoculation.--Several Northern red oak (*Quercus rubra* L.) trees with telia bearing leaves were obtained from the U.S. Forest Service Resistance Screening Center. Leaves of these trees were suspended over pH 2.2 sterile distilled water for 36 hours. Basidiospores cast from telia into the water were then concentrated and rinsed on a Millipore filter (5μm pore size) and rediluted in pH 5.5 sterile distilled water. A Coulter counter was used to adjust the concentration to 1,375,000 spores/ml. One μl drop of inoculum was placed on the upper hypocotyl region of 12 embryos from each family with a Hamilton syringe and repeating dispenser. Three uninoculated embryos/family served as controls. Inoculum was continuously agitated in an ice bath during preparation and inoculation to reduce premature germination and clumping. The embryos were incubated at $23\pm2^{\circ}C$ in darkness for two days and subsequently returned to the previously described light environment for five days.

Microscopic examination.--Embryos were harvested seven days after inoculation, fixed in FAA (formalin-acetic-acid-EtOH), dehydrated in a graded EtOH-TBA (tertiary butyl alcohol) series, embedded in paraffin, sectioned at 10μm Johansen 1940) and stained with orseillen BB and analine blue (Jewell et al. 1962). RN was rated via light microscopy using the following three scales (Gray and Amerson 1983):

1 - percentage of epidermal necrosis (RN epidermis) 0 - 100
2 - tissue necrosis (RN time)
    0 none
    1 epidermal necrosis
    2 cortical necrosis
    3 vascular necrosis
    4 pith necrosis
3 - severity of cellular necrosis (RN severity)
    0 none
    1 necrotic cytoplasm
    2 necrotic collapsed cell walls.

Gray and Amerson (1983) observed a compatible necrosis which was not associated with resistance. This type of necrosis typically developed slowly and is difficult to observe via light microscopy. Therefore, all necrosis evaluated in this study probably corresponds to the incompatible rapid type noted by Gray and Amerson (1983).

Another response characterized by the presence of a dark-red staining substance (RSS) at the inoculation point was observed and recorded. This substance was observed primarily on the epidermis but occasionally extended into the cortical region. The percentage of epidermis covered by this substance and the tissue affected (RSS epidermis and RSS tissue, respectively) were recorded using scales identical to those for the RN responses.

Data Analysis.--Phenotypic correlations among the traits measured were calculated. Field resistance at age four based on a one to five scale which was then standardized to a zero to 100 scale over several tests (Hatcher et al. 1981) were available for the eight paternal half-sib families and for 10 of the 24 full-sib families. Individual and multiple regressions of these family performance levels on the *in vitro* traits were performed. An analysis of variance appropriate for a factorial mating design was conducted and genetic parameters were estimated from the Type IV mean squares and their expected values using standard quantitative techniques (e.g., Becker 1967).

RESULTS

Phenotypic correlations (Table 1) were high (0.41 > r > 0.72) among the RN traits and between the two RSS traits (r = 0.65) as expected. RN epidermis showed negligible phenotypic correlation with the two RSS traits (r = -0.0062 and 0.046) while the other two RN traits showed weak correlations (0.19 > r > 0.27) with the RSS traits.

Table 1.-- Phenotypic correlations among *in vitro* traits

	Trait			
Trait	RN Epidermis	RN Tissue	RN Severity	RSS Epidermis
RN Tissue	0.44 0.0001[a]			
RN Severity	0.41 0.0001	0.72 0.0001		
RSS Epidermis	-0.062 NS	0.20 0.0007	0.19 0.002	
RSS Tissue	0.046 NS	0.27 0.0001	0.20 0.0006	0.65 0.0001

[a] Prob > |r| under Ho:rho = 0

Regression of rust field performance levels on the half-sib family means of individual _in vitro_ traits produced low coefficients of regression for these traits (Table 2); however, RN epidermis and RSS epidermis, both yielded moderate regression coefficients (r - square = 0.43 and 0.55, respectively). Inclusion of two and three variables simultaneously in the regression increased the regression coefficients to 0.86 and 0.94, respectively. All the _in vitro_ traits produced low regression coefficients (r - square > 0.12) when their individual full-sib means were used to predict full-sib field performance. The best three-variable-regression in this case yielded

Table 2.-- _Single and best multiple regression of rust field performance levels on half-sib and full-sib means of in vitro traits_

	Half-Sib		Full-Sib	
	r-square	Prob > F	r-square	Prob > F
RN Epidermis	0.43	0.08	0.22	NS
RN Tissue	0.093	NS	0.0052	NS
RN Severity	0.0045	NS	0.00096	NS
RSS Epidermis	0.55	0.04	0.12	NS
RSS Tissue	0.078	NS	0.044	NS
RSS Epidermis and RSS Tissue	0.86	0.006	--	--
RN Epidermis and RN Severity	--	--	0.29	NS
RN Epidermis, RSS Epidermis and RSS Tissue	0.94	0.006	0.44	NS

a moderate r-square value (0.44); however, this was not significant due to the small sample size. RN epidermis, RSS epidermis and RSS tissue compromised the best three variable regression for both half- and full-sib field performance.

Partially due to the small degrees of freedom of the "Female-Male" interaction (df = 14), the "Male" and "Female" effects in the analyses of variance were nonsignificant (Prob > F < 0.10 for all the _in vitro_ traits with the exception of the "Male" effect for RSS time. Conversely, the "Female-Male" interaction effect was significant (Prob > F < 0.10) for all the _in vitro_ traits with the exception of RSS tissue.

Several estimates of genetic variance components were negative (Table 3). Estimates of the additive genetic variances were small for the RN traits relative to their respective dominance variance estimates. The reverse phenomenon was true for the RSS traits. RSS tissue had the largest individual heritability estimate ($h_I^2 = 0.16$) due to a relatively large amount of additive variance. With a few exceptions, family heritability estimates were moderate to large ($0.35 < h^2 < 1.04$) for all traits.

Table 3.-- Estimates of genetic parameters for *in vitro* traits

Trait	Additive Variance	Dominance Variance	Individual Heritability	Half-Sib Family Heritability	Full-Sib Family Heritability
RN Epidermis	0.00843[a]	0.102	-0.049	-0.29	0.66
RN Tissue	0.0482	0.115	0.068	0.35	0.70
RN Severity	-0.00198	0.150	-0.0039	-0.026	0.54
RSS Epidermis	0.000314	-0.000376	0.045	0.37	0.12
RSS Tissue	0.0771	-0.0483	0.16	0.73	1.04

[a] Negative estimate due to sampling error. The estimate is assumed to be zero.

DISCUSSION

Gray and Amerson (in press, 1983) discussed the histology and ultrastructure of the RN response and related this response to histological reactions observed by others (Jewell and Spiers 1975, Miller et al. 1976 and Walkinshaw 1978). The composition and mode of action of the RSS response is currently unknown. RN appears to be a common response among resistant families of loblolly pine and occurred to some degree in 94 percent of the embryos observed in this study. RSS, however, was present in only 30 percent of the embryos observed. Although these two types of responses commonly occurred simultaneously, the phenotypic correlations among the traits measured indicate that the degree of development of these responses are somewhat independent. Furthermore, a relatively large portion of the genetic variance of RN appears to be due to dominance while the genetic control of the RSS response appears to be predominantly additive. Therefore, these two types of response appear to be distinct from one another.

The genetic parameters estimated from this data are not necessary representative of the loblolly pine population at large since only families with some degree of field resistance were sampled. (Half-sib field performance levels (Hatcher et al. 1981) ranged from 48 to 75). However, for the population sampled, this study has demonstrated that the RN and RSS responses possess the necessary genetic characteristics for developing an in vitro resistance screening program. The correlated response in field resistance due to selection on an in vitro trait is proportional to the genetic correlation between field performance and the in vitro trait as well as the square root of the heritability of the in vitro trait appropriate for the type of selection applied (Falconer 1960). In light of the high values for these parameters, development of a selection index based on several of these and perhaps other in vitro traits appears promising. Such an index should be based on a large number of families that are more representative of the entire loblolly pine population.

Development and implementation of an in vitro screening index could be enhanced by further reduction of the time and effort involved in assessment. For instance, it may be possible to develop a biochemical assay to detect the presence and degree of RN which is associated with compounds most likely of phenolic origin (Gray and Amerson 1983). Thus, the tedium and time involved in histological preparation and assessment could be bypassed. The RSS response is also a candidate for such an assay. Another potential enhancement would be the development of techniques to successfully infect and assess callus of loblolly pine. Select trees could be directly screened rather than their progeny. Unfortunately, to date attempts to inoculate loblolly pine callus in vitro have proven unsuccessful (Jacobi 1982).

In conclusion, the future of developing an in vitro method of screening loblolly pine for resistance to fusiform rust is promising. Coupled with the developing tissue culture technology such a method may provide the tree breeder with an effective and rapid mode of assessing substantial genetic gains in fusiform rust resistance.

NOTE: The use of trade names in this manuscript does not imply endorsement of the product named nor criticism of similar products not named.

LITERATURE CITED

Becker, W. A. 1967. Manual of Procedures in Quantitative Genetics. Washington State U. Press. Pullman, Wa., 130 p.

Carson, M. J. 1983. Breeding for fusiform rust in loblolly pine. Ph.D. thesis. North Carolina State University, Raleigh, N.C. 122p.

Falconer, D. S. 1960. Introduction to Quantitative Genetics. Ronald Press Company. New York. 365 p.

Gray, D. J. and Amerson, H.W. 1983. In vitro resistance of Pinus taeda embryos to the fusiform fungus, Cronartium quercuum f. sp. fusiforme. Ultrastructure and histology. Phytopathology (in press).

Hatcher, A. V., Bridgewater, F. E. and Weir, R. J. 1981. Performance level -- a standardized score for progeny test performance. Sil. Gen. 30:184-187.

Jacobi, W. R. 1982. Inhibition of Cronartium fusiforme by loblolly pine callus. Phytopathology 72:143-146.

Jewell, F. F. and Spiers, D. C. 1975. Histopathology of one- and two-year old resisted infections by Cronartium fusiforme in slash pine. Phytopathology 66:741-748.

Jewell, F. F., True, R. P. and Mallet, S. L. 1962. Histology of Cronartium fusiforme in slash pine seedlings. Phytopathology 52:850-855.

Johansen, D. A. 1940. Plant microtechnique. McGraw-Hill Book Co., New York, 523 p.

Miller, T., Cowling, E. B., Powers, H. R., Jr. and Blalock, T. E. 1976. Types of resistance and compatibility in slash pine seedlings infected by Cronartium fusiforme. Phytopathology 66:1229-1235.

Mott, R. L. and H. V. Amerson. 1981. A tissue culture process for the clonal production of loblolly pine plantlets. NCARS. Tech. Bull. #271, 14 p.

USDA Forest Pest Management Rep. #82-1-18. 1982, 55 p.

Walkinshaw, C. H. 1978. Cell necrosis and fungal content in fusiform rust-infected loblolly, longleaf, and slash pine seedlings. Phytopathology 68:1705-1710.

Walkinshaw, C. H., Dell, T. R. and Hubbard, S. D. 1980. Predicted field performance of slash pine families from inoculated greenhouse seedlings. USDA For. Ser. Res. Pap. 50-160.6 p.

Patterns of Genetic and Environmental Variance in a Short-term Progeny Test of Loblolly Pine

by E. C. Franklin[1]

Abstract.--Thirty-five loblolly pine families from eastern North Carolina, South Carolina and Georgia orchards of 4 companies were grown for 5 years in a short-term progeny test in Charleston, SC. The four spacings were 33, 50, 67, and 100 cm square. Each spacing consisted of 4 randomized complete blocks of sixteen-tree square plots. The objectives were (1) to determine if young trees grown at close spacing would mimic the genetic and environmental variance patterns of stands at conventional spacings at much older ages, and (2) to compare families on the basis of their competitive performance with varying numbers of sibling versus nonsibling competitors. Patterns of additive genetic variance which evolved in the closely spaced tests followed very closely those patterns found in older tests grown at conventional spacing. No differences were found in height, diameter and volume growth between groups of 8 trees containing 3, 5 or 8 sibling competitors.

Additional keywords: Short-term progeny testing, selection, heritability, *Pinus taeda* L., tree improvement, competition.

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Acknowledgements. This paper is a preliminary review of a large study which is continuing through the concerted efforts of many people. I thankfully recognize the contributions and continuing cooperation of the staff of the USDA Forest Service Research Laboratory at Charleston, SC for their diligent efforts in acquiring the data; the N.C. State Tree Improvement Cooperative for use of progeny test data; Continental Forest Industries, Savannah, GA, Union Camp Corporation, Savannah, GA, Westvaco Corporation, Summerville, SC, and Weyerhaeuser Company, New Bern, NC for supplying the seed. I recognize the large individual contributions of the two supervisory technicians who have in turn shepparded this project from its inception: William S. Dvorak and Edgar L. Davenport both formally based at Charleston, SC with the Southeastern Forest Experiment Station. Lastly, thanks to my staff for the extra effort they continue to devote to this project.

INTRODUCTION

Rate of genetic improvement of any long-lived organism can be increased by early testing and selection if certain genetic relationships exist between juvenile and mature growth phases. Most research on maturation in woody perennials concerns fruit and seed production because of the economic importance of these traits to crop yields. With commercial forest species, products are more varied and problems are compounded by less environmental control, and by the size, complexity and longevity of individual trees and stands.

Strategies for dealing with juvenile-mature phase change vary according to genetic and environmental characteristics of the traits involved. For many traits such as wood density and fiber length, careful sampling has shown that single samples at almost any age will yield good estimates of relative whole-tree values for individuals and families, because variation patterns with age are systematic and very regular. In contrast, parameters measuring growth rate are influenced by age and environment to a much greater extent. Recent research has pointed to a need for much better understanding of the effects of age and associated stand environment on juvenile-mature relationships.

Analyses of long-term progeny tests of four North American conifers led to the development of a hypothetical model to describe genetic phase changes in the growth of stands (Franklin, 1979). The model divides stand development into three genetic phases based on the behavior of the additive genetic variance and the heritability of the trait (Fig. 1). The juvenile genotypic phase is characterized by extremely low levels of additive genetic variance with a peak in heritability (juvenile genetic culmination) in the early to middle part of the phase. The mature genotypic phase is characterized by rapidly increasing additive genetic variance and heritability with a peak in heritability (mature genetic culmination) occuring early in the phase . The codominance-suppression phase is characterized by a rapid decline in additive genetic variance and an especially rapid decline in heritability as mortality removes suppressed trees and the stand approaches uniformity in stocking, and heights of dominants and codominants.

Recent results show that levels of additive genetic variances for height, diameter and volume growth vary widely but systematically in the course of stand development (Namkoong _et al_. 1972, Namkoong and Conkle 1976, Franklin 1979). The implication of these results for selecting in natural stands and plantations at conventional spacing is that selection should be done around half-rotation age. In the hypothetical model, this is called the mature genotypic phase (Franklin 1979). A much greater rate of genetic gain per unit time could be obtained if selections could be done at younger ages. Because trees are so plastic in their growth response to environmental influences, particularly spacial relationships, I developed the hypothesis that stands of trees growing close together might simulate stand development at very young ages typical of more widely spaced stands at much older ages. From a practical point of view, once a poorly competing family falls behind, it never catches up. So why wait ten to twenty years at conventional spacing to develop enough competition to make that happen?

METHODS

The experimental design consisted of four separate trials grown at 33, 50, 67, and 100 cm square spacings in a small agricultural field at the USDA Forest Service Laboratory in Charleston, SC. Each trial contained 4 replications of 35 16-tree square family plots. The families were orchard open-pollinated from four companies in North Carolina, South Carolina and Georgia (Table 1). Clones were chosen on the basis of having been crossed with large numbers of other clones and of having 12- to 16-year measurements in progeny tests at conventional spacings.

Table 1.--Companies which made seed available from selected clones in their commercial production orchards

Company	No. Families	Provenance
Continental Forest Industries	8	GA Piedmont
Union Camp Corporation	8	GA/SC Coastal Plain
Weyerhaeuser Company	14	NC Coastal Plain
Westvaco Corporation	5	SC Coastal Plain
	35	

Families totaling about 12,000 trees were grown as container stock in a greenhouse and outplanted in early June, 1978 at 12 weeks of age. The site was prepared by raking and disking; only grasses remained on the site. Survival was generally good but some replacement planting was done during the first 6 months of the study. Competition from grasses was controlled until crown closure by mowing in the 100-cm spacing and with herbicides in the closer spacings. Soil tests indicated no fertilization was needed. Infestations of spider mites and tipmoths were controlled with periodic spraying of insecticides.

Measurements of total height were made during the second through the ninth growing months over a five-year period. December, January and February were classified as non-growing months and excluded from the measurement schedule. Measurements in the 10th through the 19th growing months included height and diameter. Diameters were measured first at one inch above the ground (10th month) then at mid-height (15th through 23rd growing months) and from then on at 4 1/2 feet above ground. Heights and diameters were measured in alternate growing months in the 21st through the 37th growing months. An index of volume equal to diameter squared times height was used.

Cumulative mortality, total phenotypic variance, additive genetic variance, environmental variance, and heritability were estimated for each measurement. Variances were interpreted based on the simpliest additive model:

$$P = A + E, \quad \text{and} \quad h^2 = \frac{A}{P},$$

where:

P is phenotypic variance,

A is additive genetic variance,

E is environmental variance, and

h^2 is individual tree, narrow-sense heritability.

RESULTS

Mortality

Cumulative mortality did not begin to reflect large differences in growing space until the fourth and fifth years of the study. In 1981, the amount of mortality sharply increased in the 33-cm spacing, and in 1982 in the 50-cm spacing (Table 2).

Genetic Variances

The rapid increase in additive genetic variance, marking the juvenile/mature phase change (as interpreted based on Fig. 1), occurred in the 9th growing month for height and the 21st growing month for diameter and volume in all spacings (Table 3). Similarly, highest heritability in the mature genotypic phase (mature genetic culmination) occurred at 15 months for height and 23 months for diameter and volume in all spacings except 21

Table 2.--Culmulative mortality percentages by spacing and growing season

	SPACING (CM)			
YEAR	33	50	67	100
	Percent			
78	2	2	1	2
79	4	3	2	5
80	9	4	2	6
81	43	8	4	6
82	67	22	12	10

Table 3.--Number of growing months to reach the juvenile/mature phase change as interpreted based on the model by Franklin (1979)

	SPACING (CM)			
TRAIT	33	50	67	100
	Months			
Height	9	9	9	9
Diameter	21	21	21	21
Volume[a]	21	21	21	21

[a] Volume index based on diameter squared times height.

months for volume at 33-cm spacing (Table 4). The mature genetic culmination heritability was highest for height, with the two intermediate spacings yielding the highest values. Heritabilities for diameter and volume were lowest at the 33-cm spacing and trended higher at the wider spacings (Table 5). All heritabilities steadily decreased after reaching the mature genetic culmination, except heritability for height at the 100-cm

Table 4.--Number of growing months to reach mature genotypic (maximum heritability) as interpreted based on the model by Franklin (1979)

TRAIT	SPACING (CM) 33	50	67	100
	Months			
Height	15	15	15	30[a]
Diameter	23	23	23	23
Volume[b]	21	23	23	23

[a] In the 100-cm spacing, a sharp, distinct peak occurred at 15 months, but a rounded, less distinct peak which was .05 units higher, ocurred at 30 months.

[b] Volume index based on diameter squared times height.

Table 5.--Heritability at mature genotypic culmination as interpreted based on the model by Franklin (1979)

TRAIT	SPACING 33	50	67	100
	Heritability			
Height	.73	.87	.90	.70
Diameter	.37	.45	.64	.60
Volume[a]	.36	.50	.60	.63

[a] Volume index based on diameter squared times height.

spacing.[2] For height this was a period of 22 growing months over 3 seasons, and for diameter and volume, a period of 14 growing months over 2 seasons (Figs. 2, 3, 4).

The 16-tree square plots provided a test for trends in competitive influence of sibling versus nonsibling neighbors.

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[2] In the 100-cm spacing, a sharp, distinct peak occurred at 15 months, but a rounded, less distinct peak which was .05 units higher, occurred at 30 months.

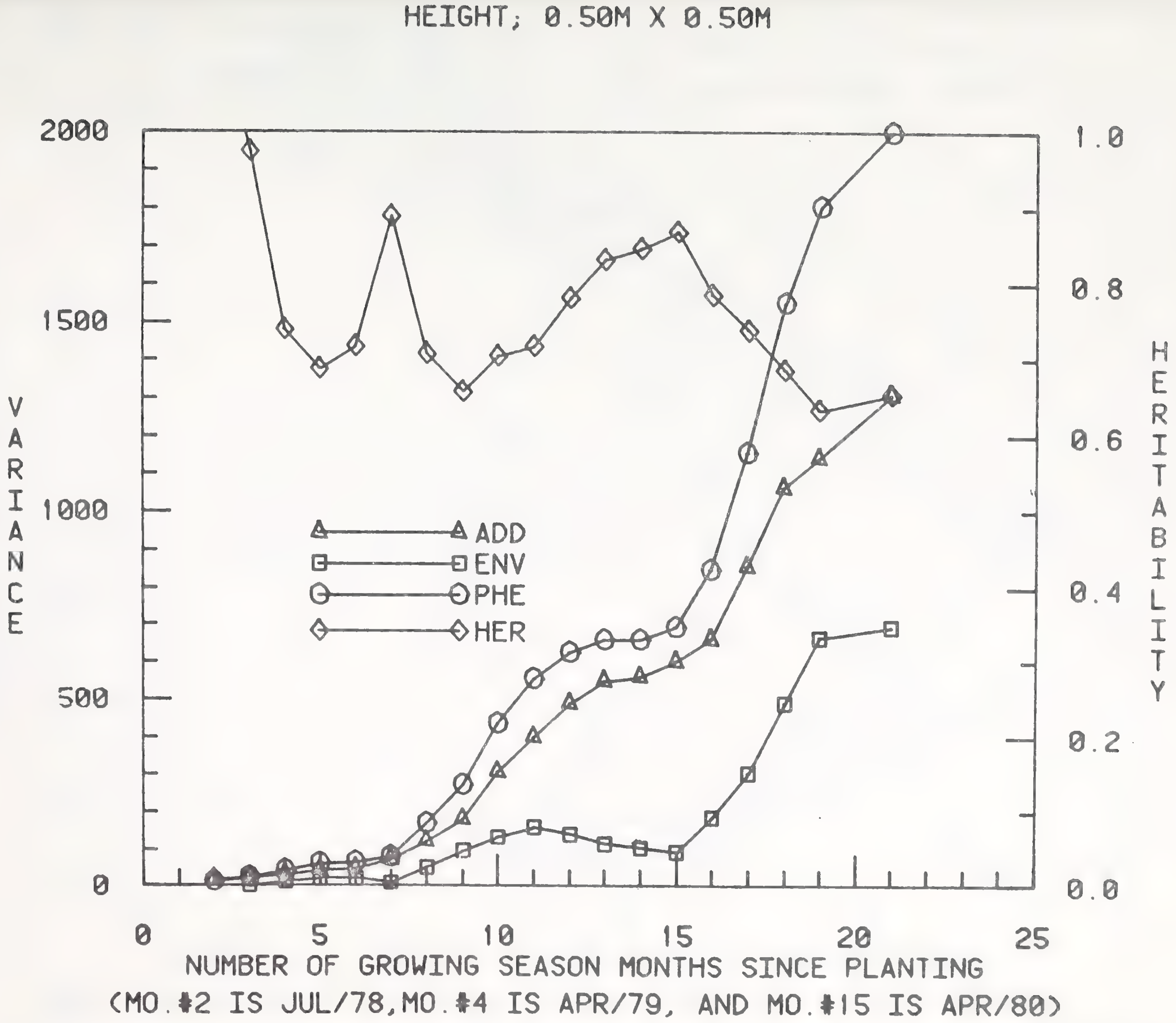

Figure 2.--Trends in the additive (ADD), environmental (ENV), and phenotypic (PHE) variances, and in the heritability ratio (HER = ADD/PHE) of height of 35 loblolly pine families growing at a 1/2-meter square spacing through 37 growing months.

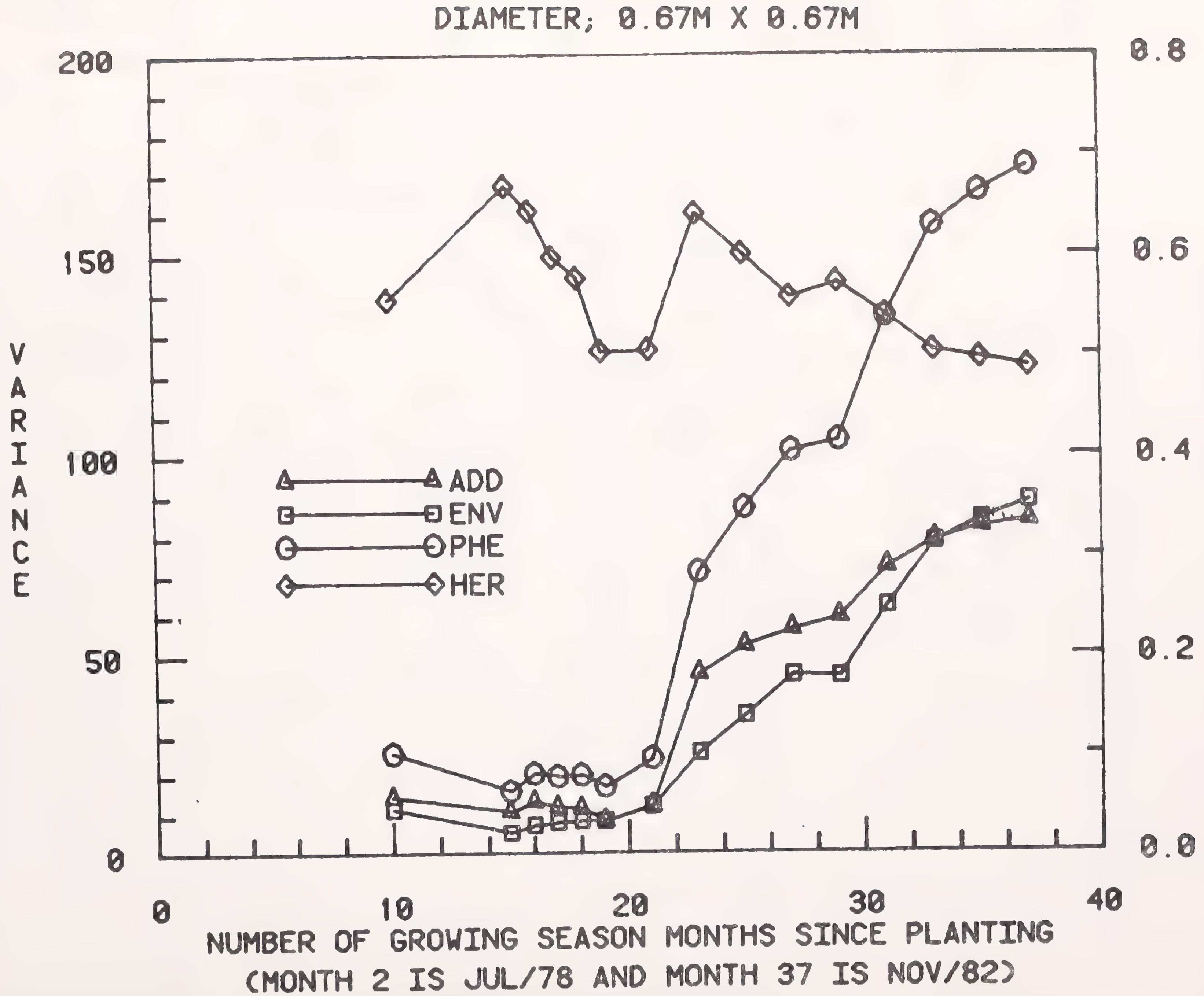

Figure 3.--Trends in the additive (ADD), environmental (ENV), and phenotypic (PHE) variances, and in the heritability ratio (HER = ADD/PHE) of diameter of 35 loblolly pine families growing at a 2/3-meter square spacing through 37 growing months.

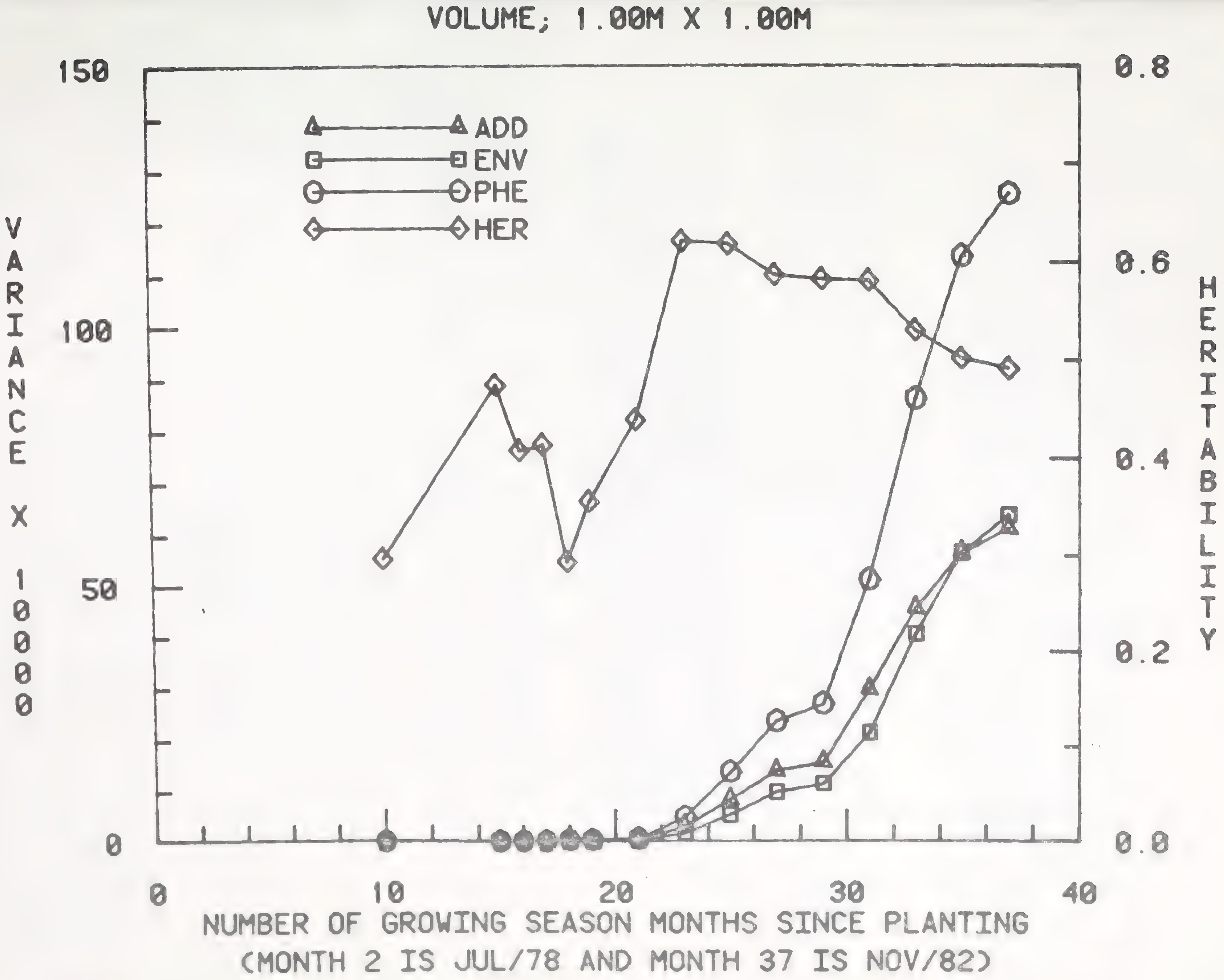

Figure 4.--Trends in the additive (ADD), environmental (ENV), and phenotypic (PHE) variances, and in the heritability ratio (HER = ADD/PHE) of volume of 35 loblolly pine families growing at a 1-meter square spacing through 37 growing months.

The 4 corner trees had 3 sibling and 5 nonsibling competitors. The 8 internal trees on the outside rows had 5 sibling and 3 nonsibling competitors. The 4 internal trees had all sibling competitors (Fig. 5). Analyses of variance were run for all traits and spacings at 37 months and repeated for the 33 cm spacing at 25 months. Results showed no differences between sibling competitor groups. Regression of growth parameters on increasing numbers of sibling competitors per group failed to demonstrate any trends.

DISCUSSION

The hypothesis under test was that for purposes of genetic interpretaion and testing, families of trees grown at very close spacings in a short period of time would mimic the development of stands of those same families grown at conventional spacing, over a much longer period of time.

Under this hypothesis based on the model (Fig. 1), the following would be expected if the hypothesis was acceptable:

1. A distinct phase change from the juvenile genotypic to mature genotypic phase marked by a rapid increase in additive genetic variance from a level hardly varying from nil.

2. A relatively high but decreasing heritability in the juvenile genotypic phase.

3. A very rapid rise in heritability to a distinct peak early in the mature genotypic phase, then a gradual decline toward the codominance-suppression phase change.

4. A sharp decline in additive genetic variance marking the boundary of the codominance-suppression phase accompanied by a plummeting heritability.

With only one minor exception (footnote 2), trends for each trait at each spacing fit perfectly through item 3. Thus, the results obtained so far are consistent with the hypothesis, but are inconclusive, because results have not reached the boundary of the codominance-suppression phase.

Comparing the behavior of the variances for the short-term tests with those of the longer-term tests, the scale indicates that development in the short-term test is well into the mature genotypic phase. Indeed, the rapid decline of the additive genetic variance is expected to occur soon. The closer the spacing the sooner the decline is expected. At the 33-cm spacing, 15% of the families have 10 or fewer trees remaining out of the original 64. When whole families start dropping out, the

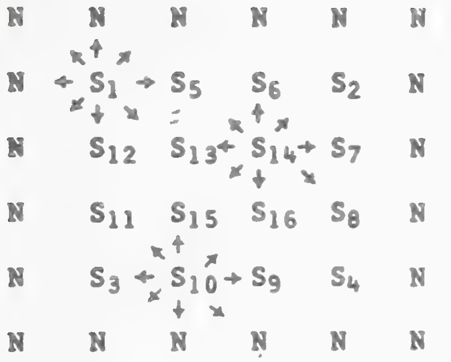

Figure 5.--Competitive spacial relationships between sibling and nonsibling trees with a 16-tree square plot: $S_{1,2,3,4}$ have 3 sibling 5 nonsibling competitors; $S_{5,6,7,8,9,10,11,12}$ have 5 sibling, 3 nonsibling competitors, $S_{13,14,15,16}$ have 8 sibling competitors.

additive genetic variance is expected to plummet. This trend is expected in each spacing as mortality increases (Table 2).

These results are interesting but what is the practical significance of short-term testing? Can these tests be used to pick families which are genetically superior under conventional silvicultural regimes? This topic will be developed in a subsequent paper. Preliminary results indicate that short-term tests will be useful but that the choice of parameters to express superiority will be critical. More emphasis must be placed on yield per unit area rather than individual tree superiority or the superiority of families based on the average tree. For example, a family which combines fast growth and good survival against competition is expected to produce somewhat smaller but more uniform trees and higher yields per unit area than a family with poor or erratic survival leading to production of a few large trees. If silvicultural techniques such as planting at wide spacing are to be used, where competition is not an important environmental parameter, short-term tests at close spacing may not be appropriate in the development of genetic strains for that use.

Sibling Versus Non-sibling Competitive Ability

The apparent lack of differences between groups of trees with varying numbers of sibling versus nonsibling competitors is not unexpected with the relatively low level of genetic control obtained with orchard open-pollinated families. With full-sib families real effects may be found, and with certain clonal combinations real effects will almost certainly be found. Whether those effects will be large enough to be important remains to be demonstrated.

LITERATURE CITED

Franklin, E. C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Sil. Genet. 5-6: 207-212.

Namkoong, G. and Conkle, M. T. 1976. Time trends in genetic control of height growth in ponderosa pine. For. Sci. 22:2-12.

Namkoong, G., R. A. Usanis, R. R. Silen. 1972. Age-related variation in genetic control of height growth in Douglas-fir. Theor. and Appl. Genet. 42:151-159.

POSTER SESSION ABSTRACTS

INCREASE AND SPREAD OF BROWN SPOT NEEDLE BLIGHT WITHIN SINGLE AND MULTIPLE FAMILY PLANTINGS OF OPEN-POLLINATED LONGLEAF PINE

Margene M. Griggs[1]

Longleaf pine (Pinus palustris Mill.) plantings were established in south Mississippi and southwest Georgia to study the increase in time and space of brown spot needle blight, caused by Scirrhia acicola (Dearn.) Siggers. Open-pollinated families with varying degrees of resistance to brown spot were planted in single- and multiple-family plots. Epidemics were initiated by placing severely infected longleaf pine needles on susceptible longleaf source plants in the center of the plots. Disease was measured at 6-week intervals for two growing seasons. Disease progress curves were constructed from these measurements. Disease achieved higher levels in Georgia than in Mississippi. Lesion numbers fluctuated considerably during the course of the epidemics. Curve elements of percent needle dieback progress curves were useful to compare families. Resistant families delayed the onset of needle dieback by as much as 5-7 weeks, had fewer numbers of lesions, and had lower levels of maximum dieback. The rate of needle dieback/week (YRATE) varied by distance from the initial infection focus but there were no significant family or location differences (YRATE = .026-.033). The rate of pathogen movement outward from initial infection foci was similar for all families and for both locations. Isopaths of lesion numbers moved outwardly (or centrifugally) from center of plots at rates of 0.05 m/wk, while isopaths of needle dieback averaged 0.13 m/wk. The mixing of resistant and susceptible families did not mitigate the BSNB epidemic as factors favoring auto-infection predominated over those favoring allo-infection. Ninety-nine percent of all trees were out of the grass stage by the end of the second growing season. Family means of second-year height ranged 28-47 cm in Mississippi and 30-37 cm in Georgia. Correlation between percent maximum needle dieback and second year height at each location was not statistically significant (Mississippi: $r = -0.46$ and Georgia: $r = -0.45$).

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A TRIAL TO MECHANICALLY SORT CLONES FROM A BULK SEED LOT

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Increasing numbers of organizations are harvesting loblolly pine seed with net collection systems instead of collecting cones. With this type of bulk seed collection, the benefits of genetically uniform seed are forfeited. These benefits include more uniform germination, more uniform spacing of seed on the nursery bed, and ultimately more plantable seedlings per pound of seed. Differences among clones in seed diameter, weight, and color are familiar to anyone who has worked with individual tree collections of seed. A trial was made to determine if precision seed sizing could separate clones from a bulk seed lot.

Ten clones were collected from each of 20 clones in a seed orchard in South Carolina. The seed was kept separate by clone after extraction. Each clonal lot was sized with round hole screens. (Round hole screens separate seed by their diameters.) The empty seed was removed with a column blower. Total weight for each fraction within each clone was obtained, and also the weight of 100 seed from each fraction within a clone. A germination test of 100 seed was conducted on each screen fraction within clones. Days to 90 percent of total germination were computed.

Sizing the seed with screens did not separate the clones effectively. The total weight of the screen fractions showed that if all clones had been bulked together most clones would have contributed no less than 5 percent of the weight of each seed size. Weights of 100 seed from each screen size showed that weight separations following screen sizing still would not separate the seeds into clonally pure lots. Days to 90 percent of total germination was not related to either screen size or 100 seed weight, but was strongly associated with clone. Sizing seed with round hole screens and by weight is of value for more uniform placement of seed in the nursery, but cannot necessarily be relied on for recovery of clonally pure lots. Weight separations within a screen size can produce sublots with fewer numbers of clones. With these 20 clones, the weight separations probably would produce fractions containing 5 to 7 clones. Other seed orchards might present a different situation and the reader is cautioned not to generalize the results of this trial.

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FOREST CROP IMPROVEMENT BY TISSUE CULTURE

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Existing methods of selection followed by seed orchard production of seeds requires 17 years and can yield a 32% value increase. Currently, methods are developing for the clonal production of forest trees (Southern conifers) via tissue culture. Existing tissue culture methods generally are applicable only to juvenile trees and the number of individuals within the clone is small, so large gains predicted for clonal forestry are not yet attainable. Nevertheless, these current methods are precursors for callus mediated mass propagation systems of the near-term future which can yield massive gains. Protoplast technology and *in vitro* breeding and selection offer a pathway to rapid production of genetically improved individuals which may be multiplied by emerging propagation techniques.

POPULATION GENETIC STRUCTURE OF THE DOUGLAS-FIR SHELTERWOOD REGENERATION SYSTEM IN SOUTHWEST OREGON

David Neale
Oregon State University

Knowledge of the population genetic structure of natural populations of forest trees is important for the efficient domestication and management of these populations. Shelterwood is used widely in southwest Oregon and is a good experimental system for population genetic studies. There were three objectives in this study to elucidate the determinants of population genetic structure of these Douglas-fir shelterwoods: 1) Access the levels of genic diversity in the life cycle of shelterwood stands; 2) Quantify the mating system; and 3) Investigate mechanisms for family structure in shelterwood regeneration. Genic diversity is fairly constant throughout the life cycle of these shelterwoods, although there is evidence for some inbreeding in the natural regeneration of one stand. The outcrossing rate is high (.90-1.00) in both shelterwoods and uncut stands, but there is evidence that selfing increases with lower plant density. Seed and pollen are dispersed an average of 50m and 70m, respectively, within shelterwood stands. The effective population size was estimated to be approximately 35 trees. Large within stand variability, outcrossing, and seed and pollen dispersal maintain genetic diversity in regenerated shelterwoods and prevent significant population subdivision within individual stands.

ADVENTITIOUS SHOOT FORMATION ON EMBRYOS OF PINUS PALUSTRIS MILL., P. ELLIOTTII ENGELM. AND P. PALUSTRIS X ELLIOTTII.

Michael Stine and Harry E. Sommer
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Abstract. Adventitious shoot formation on the embryos of longleaf pine (*P. palustris* Mill.), slash pine (*P. elliottii* Engelm.) and their hybrid (*P. palustris* x *elliottii*) were compared. Using modified procedures of Reilly and Brown (1976), entire mature embryos were placed in a liquid media of Blaydes major salts, iron as Fe-EDTA, minor salts of Brown (Sommer and Brown, 1980), Doy's vitamins and 2% sucrose. The media was supplemented with napthaleneacetic acid at concentrations of 0.1, 0.01 and 0.001 mg./l. and 6-benzylaminopurine at concentrations of 1, 5, 10, 15 and 20 mg./l. The experimental design was a 3x5 factorial, with 20 explants of each species established for each hormone combination. The embryos were kept in the liquid media for ten days and then were transferred to a solid media of the following composition: major salts of Risser and White at half-strength, iron as Fe-EDTA, minor salts of Brown, Doy's vitamins, 1% sucrose and 0.6% Phytagar.

Adventitious shoots first appear on raised areas of the epidermis of the cotyledons of longleaf pine and the hybrid after 3-4 weeks in culture. Shoots form along the entire length of the cotyledon, with the fastest elongation of needles occurring on shoots located on the most distal portion of the cotyledon. With slash pine, most of the adventitious shoots form near the tips of the cotyledons, with only occasional formation elsewhere. A few of the slash pine embryos formed adventitious shoots on their hypocotyls, while longleaf pine and the hybrid did not. The experiment is still ongoing and at present it is not possible to identify the optimal concentrations of hormones for adventitious shoot initiation.

Scanning electron microscopy (SEM) was used to examine the organization and surface morphology of adventitious shoots. Samples were fixed in 2% glutaraldehyde/0.1 M cacodylate buffer, dehydrated with an ethanol series, critical point dried with CO_2 and coated with gold/palladium prior to viewing with a Cambridge Stereoscan Mark 2A. SEM showed the adventitious shoots of longleaf pine and the hybrid, to form on raised areas of the epidermis of the cotyledons, while in slash pine, shoot formation was not limited to raised areas. Stoma were found on the needles of adventitious shoots of longleaf and slash pine (the hybrids yet examined are younger, and stomata have not yet been found after 5-7 weeks in culture) after 11-12 weeks in culture. The stoma form in rows and appear to be occluded with epicuticular wax.

Literature Cited

Reilly, K. J. and C. L. Brown. 1976. In vitro studies of bud and shoot bud and shoot formation in *Pinus radiata* and *Psuedotsuga menziesii*. Georgia Forest Research Paper No. 86.

Sommer, H. E. and C. L. Brown. 1980. Embryogenesis in tissue cultures of sweetgum. For. Sci. 26: 257-260.

IN VITRO PROPAGATION OF LIQUIDAMBAR STYRACIFLUA L.

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We reported on the propagation of Sweetgum (Liquidambar styraciflua L.) by tissue culture at the 16th Southern Forest Tree Improvement Conference (P. 184-188). A modified Risser and White's medium with 0.01 PPM NAA and 0.5 PPM BA, solidified in agar, yielded 2.1 to 3.9 buds differentiated on organogenic hypocotyl sections. Only about 33% of the buds reached the plantlet stage. Recently we have improved on the method by explanting the hypocotyl sections onto modified Risser and White's medium with 1 PPM IAA and 5 PPM 2iP and agar. As before, only a few buds were differentiated on organogenic hypocotyl sections. However, when transferred to a liquid Blaydes' media with 0.01 PPM NAA and 0.5 PPM BA, numerous shoots were differentiated. A single harvest of shoots from a 125 ml flask ranged from 25-100 shoots. With repeated harvest over the period of 1 year as many as 571 shoots have been obtained. More than 90% of the shoots obtained from liquid culture root on basal modified Risser and White's medium.

The anatomy of the plantlets and shoots obtained by both methods have been studied in relation to prospects for hardening-off the plantlets. Observations using light, scanning and transmission electron microscopy showed differences in general morphology of the leaves. Plantlets differentiated on agar had atypical anatomical characteristics which we have reported (Amer. J. Bot. 69:1579-1586). Leaves of plantlets on agar had undifferentiated mesophyll cells with extensive intercellular spaces, large vacuoles, flattened chloroplast with an irregularly arranged internal membrane system, and superficial, circular stomata. Shoots differentiated in liquid culture, however, had characteristics more like noncultured plants. Leaves of liquid cultured shoots had a more compact mesophyll, although a palisade layer was still not differentiated. Chloroplast had evident grana and stomata were flattened and ellipsoid.

Our system of liquid culture has several advantages over previous agar methods. A much more rapid shoot multiplication rate is possible and high rooting percentages have been obtained. In addition, shoots differentiated from liquid culture appear more typical structurally and plantlets from these shoots are expected to be more easily acclimatized.

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WIDE CROSSES TO IMPROVE FUSIFORM RUST RESISTANCE IN SLASH PINE

C. H. Walkinshaw and M. M. Griggs[1]

Wide geographical (Florida-Louisiana) crosses were made among resistant slash pine (*Pinus elliottii* Engelm. var. *elliottii*) parents in the Gulf South. Full-sib progeny were inoculated with two single gall collections of *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme*. One collection is known from previous work to be less pathogenic than average. The other has been consistently more pathogenic in our studies. Inoculations of 48 full-sib families and 33 wind-pollinated checks were made at Gulfport, Mississippi, or at the Resistance Screening Center at Asheville, North Carolina. Percent galled ranged from near 0 to more than 80 (Table 1). Gall-free survivors have been outplanted to verify their disease-free condition and to serve as potential future breeding material. Inheritance of resistance appears to be additive and quantitative as reported earlier by this laboratory. Wide crossing of moderately resistant commercial slash pines with highly resistant selected individuals is a viable approach to obtaining satisfactory planting stock for areas where fusiform rust is severe.

Table 1.--*Percent galled slash pine seedlings 9 months after inoculation with a highly pathogenic single gall collection of C. quercuum f. sp. fusiforme*[a]

Experiment number					
1		2		3	
Cross	%	Cross	%	Cross	%
8-7 x 18-55	34	8-7 x 36-55	42	LA-11 x 24-54	3
8-7 x 24-54	42	18-27 x 36-55	56	9-2 x 36-55	17
8-7 x 71-58	36	8-7 x Wind	78	LA-11 x Wind	2
8-7 x Wind	67	18-27 x Wind	75	24-54 x Wind	40
18-55 x Wind	72	36-55 x Wind	83	9-2 x Wind	26
24-54 x Wind	50			36-55 x Wind	31
71-58 x Wind	75				

[a] Means for 3 replications of 12 seedlings grown in a greenhouse. Results for Forest Service and Buckeye Cellulose Corporation crosses only.

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[1] Principal Plant Pathologist and Plant Geneticist, respectively, USDA Forest Service, Southern Forest Experiment Station, P. O. Box 2008, GMF, Gulfport, MS 39503.

GEOGRAPHIC VARIATION IN LOBLOLLY PINE

17th SFTIC Poster Abstract

O. O. Wells
Southern Forest Experiment Station

Incorporating geographic variation in loblolly pine into existing tree improvement programs is gaining more attention as the older provenance tests mature and instances where gain can be made by choice of non-local seed sources are demonstrated.

Twenty-five year results in a test of 36 seed sources in southern AR showed that early height differences between eastern and western sources, evident since the fifth year, continued to diverge, with consequent volume differences of about 30 percent near rotation age. The rangewide sources proved to be well adapted in southern Arkansas except for those from near the Gulf Coast and Florida. Source latitude was very important to adaptation, source longitude was not. Eastern loblolly has been planted on an operational basis in Arkansas and Oklahoma for several years.

Use of Livingston Parish and East Texas loblolly 600 to 800 miles east of its origin in high rust hazard areas is another application of geographic variation that is becoming standard procedure in southern forestry.

The challenge for people applying these geographic variations commercially is to integrate them with existing tree improvement programs so that they add to genetic gain based on individual tree variation in local populations.

HISTORY OF S.F.T.I.C. AND RESEARCH PRIORITIES QUESTIONAIRE

Southern Forest Tree Improvement

Problems and Research Priorities - June, 1983

O. O. Wells, David Bramlett, Susan Kossuth - Ad Hoc Committee

The Conference Chairman asked the ad hoc Committee to poll the attendees about their perceptions of researchable problems facing southern forest tree improvement and about the priority that should be assigned each of these problems. Accordingly, we circulated a questionnaire at the conference that listed 16 appropriate items and asked each attendee to add items if necessary and to rank any or all of these in order of priority. A similar survey had been carried out in 1973 at the 12th SFTIC and it was desired to compare the perception of problems and priorities 10 years later as well as to produce some useful data for planners of Forest Tree Improvement research in the South.

Of the approximately 200 registrants, 94 responded. We calculated the average rank assigned to each of the 16 items printed on the questionnaire and merely listed the additional items that were volunteered.

All respondents did not rank all 16 items so an adjustment was necessary to arrive at average rank. We assumed that unranked items were considered lower priority than ranked ones and then assigned a single low rank to the items each respondent left unranked.

Results were as follows (Table 1). Items are listed in descending order of priority (1 = highest priority, 16 = lowest).

Advanced generation pine breeding strategies headed the list by a considerable margin reflecting the fact that most southern programs are into at least the second generation. Concern about direction of the breeding in the future is obviously high.

The high average ranking of juvenile-mature correlations probably reflects the often-expressed concern with early testing, so that we "turn over" generations more rapidly.

Fusiform rust resistance breeding, seed orchard management, including cone and seed insect control, ranked high as did vegetative propagation which has had a period of intense publicity recently.

It is noteworthy that competition effects and incorporation of genetic effects into growth and yield models attained average rank even though work in these areas is quite new in forest genetics. There must be a fairly widespread awareness that genetic gain in growth rate is expressed through a process of stand-dynamics and that growth and yield methods are going to be necessary to relate row-plot progeny test data to actual yields.

Table 1.--Priority ranking (high to low) assigned to 16 research categories by attendees at 17th SFTIC (1983).

RESEARCH CATEGORY	$\overline{X}$ RANK
ADVANCED GENERATION PINE BREEDING STRATEGIES	5.3
JUVENILE - MATURE CORRELATIONS	6.5
FUSIFORM RUST RESISTANCE BREEDING	6.7
CONE AND SEED INSECT CONTROL	7.2
SEED ORCHARD CULTURE	7.3
VEGETATIVE PROPOGATION	7.4
COMPETITION EFFECTS	7.6
GENETIC EFFECT INTO GROWTH AND YIELD MODELS	8.1
REPRODUCTIVE PHYSIOLOGY	8.4
CONE AND SEED HARVESTING	8.6
POLLEN MANAGEMENT	9.6
HARDWOOD GENETICS AND BREEDING	9.8
GEOGRAPHIC VARIATION	10.0
GENE CONSERVATION	10.2
HYBRIDIZATION	10.7
BROWN SPOT NEEDLE BLIGHT RESISTANCE	12.7

The volunteered items (Table 2) could not be assigned average rank with the items printed on the questionnaire but it was obvious that genetic engineering was considered of some importance. We included respondents listing cytogenetics, gene mapping, molecular genetics, and genetic engineering itself in this category.

Table 2.--Research categories volunteered by 94 respondents at 17 SFTIC (1983)

RESEARCH CATEGORY	NUMBER MENTIONING
GENETIC ENGINEERING	6
PITCH CANKER CONTROL IN ORCHARDS	4
EARLY TESTING	3
ACCELERATED BREEDING	3
ASSESSING SELECTION PROGRESS	1
SELECTION INDEX	1
THINNING PROGENY TESTS	1
OPERATIONS RESEARCH - LINEAR PROGRAMMING	1
DISEASE RESISTANCE	1
YIELD PHYSIOLOGY	1
ORCHARD DESIGN	1
SEED EXTRACTION AND CONE RIPENESS	1

Ten years ago, when the first generation orchards were just beginning to produce seed, cone and seed insect control headed the list of concerns of attendees at the 12th SFTIC (Table 3).

Table 3.--Proportion of respondents listing nine research categories in response to a questionnaire on research priorities circulated at the 12th SFTIC (1973)

RESEARCH CATEGORY	Proportion of respondents listing
	%
CONE AND SEED INSECT CONTROL	63
REPRODUCTIVE PHYSIOLOGY	38
HARDWOOD GENETICS AND BREEDING	30
ADVANCED GENERATION PINE BREEDING STRATEGIES	28
CONE AND SEED HARVESTING METHODS	24
FUSIFORM RUST RESISTANCE BREEDING	23
PINE POLLEN MANAGEMENT	23
FOREST GENE RESOURCE CONSERVATION	15
JUVENILE/MATURE CORRELATIONS	9

Reproductive physiology was in second place. Presently, both these items are perceived to be of lesser importance by SFTIC attendees. Seed supply is apparently less of a problem now as a result of maturing orchards and development of effective insect control measures. Hardwood genetics has also declined in priority ranking over the past 10 years while juvenile-mature correlations went from the bottom to the top of the list during the same period.

THE SOUTHERN FOREST TREE IMPROVEMENT COMMITTEE, 1971-81

A. E. Squillace[1]

Abstract.--A history of the activities of the Southern Forest Tree Improvement Committee during the period 1971-81 is presented. Included are committee organization and operational policy, accomplishments and services, subcommittee activities, membership, officers, meetings, and conferences sponsored.

Additional keywords: History, forest genetics.

Thirty years ago the development of superior trees was little more than a dream. Many plans were made and some work was started, but no one was sure that appreciable genetic gains could be made or that such gains could be attained at reasonable costs. Today tree improvement is a reality and a major phase of forestry. This is especially true in the South. According to a survey made by the USDA Forest Service (1982), of the 13,618 acres of seed orchard established in the U.S. up to 1981, 78 percent were in the South. Most of the forestry organizations in this region now have tree improvement programs and many have seed orchards sufficient to supply all the seeds they need for forest planting. Estimated genetic gains are usually substantial.

There is no doubt that the tremendous progress made was due partly to the efforts of the Southern Forest Tree Improvement Committee, which was organized in 1951. This report gives a brief history and summary of activities of the Committee during the period 1971-1981, with some reference to previous activities. Previous historical accounts were given by Ostrom (1953), Kaufman (1954), and Kaufman (Committee sponsored publication No. 32)[2], the latter covering the period 1951-1971.

COMMITTEE ORGANIZATION AND OPERATIONAL POLICY

Present objectives of the Committee are essentially the same as those adopted in 1952:

1. To advise and assist those interested in the improvement of southern forest trees in arranging for and conducting research and development programs.

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[1] Adjunct Professor, School of Forest Resources and Conservation, University of Florida and Volunteer, USDA Forest Service.

[2] Committee sponsored publications, listed in Appendix E, will henceforth be cited by showing publication numbers in parentheses. Other publications, listed under "Literature Cited," will be cited in the usual manner.

2. To provide a clearinghouse for information on forest tree improvement.

3. To provide for or assist in coordination in the conduct of a southwide program for tree improvement research and development.

4. To foster and encourage the advancement of knowledge of southern tree genetics.

The Committee has no formal constitution or by-laws, but operates under a statement of operational procedures which has been modified several times. In 1971, the "Organization, Policy, and Procedures of the Southern Forest Tree Improvement Committee, Revised September 1968" were in effect. Essential features, along with subsequent revisions, are outlined below.

1. Committee membership and rotation was restructured in 1976, mainly to include representation of cooperative tree improvement programs. At this time it was also decided that the Committee would designate one of the three forestry school appointees to represent Cooperative State Research Service (CSRS) Regional Project S-23, and that the Pathology appointee would represent CSRS Regional Project S-100, in order to maintain better liaison with these research organizations. Representation of Forest Farmers Association was discontinued in 1978. The name of the "Southern Pine Association" was changed to "Southern Forest Products Association" in 1970. Pollen management and cone harvesting specialists were incorporated in 1977 and 1979, respectively. Membership structure (24 members) in 1981 is given in Table 1. Terms of members begin on June 1 and end May 31 of the years specified. Members serving between 1971 and 1981 are listed in Appendix A.

2. Officers consist of Chairman, Vice-Chairman, and Secretary. They are elected by the Committee and serve 2-year terms. They, along with the past chairman or a member at large, serve as the Executive Committee, which handles mainly interim routine business. Officers during 1951-1981 are shown in Appendix B.

3. Committee meetings were usually held biannually through 1960, at which time it was decided to hold them annually with the provision that special meetings could be called as required (Appendix C).

4. Southwide conferences have been held biennially (Appendix D).

5. Affiliation with the Forest Genetics Research Foundation (apparently inadvertently included in the 1968 Revised Procedures) ceased in 1961, following extinction of the Foundation. Also, service of the Committee as advisor to the Southern Institute of Forest Genetics ceased in 1965.

Table 1.--Southern Forest Tree Improvement Committee representation and period of tenure by agency or interest, as of 1981.

Agency or specialty represented	Number of Representatives	Appointers
	GROUP A--6 YEAR TERMS[a]	
Pulp and paper industry	3	Director, Southern Forest Institute
State forestry agencies	3	Chairman, Southern Group State Foresters
Forestry Schools	3	Assoc. of South. Coll. and Univ. For. Res. Organ., South. Region
Hardwood Research Council	1	Research Coordinator of the Council
Southern Forest Products Assoc.	1	Vice-president of the Association
	GROUP B--INDEFINITE TERMS	
Southeast. For. Exp. Stn. USDA For. Serv.	1	Director of the Station
South. For. Exp. Stn. USDA For. Serv.	1	Director of the Station
Southeast. Area, State and Private For., USDA For. Serv.[b]	1	Area Director[b]
Tennessee Valley Authority	1	Chief, Division of Land and Forest Research, TVA
	GROUP C (SPECIALISTS)--6 YEAR TERMS[a]	
Geographic variation	1	Southern Forest Tree Improvement Committee
Forest pathology	1	Southern Forest Tree Improvement Committee
Forest entomology	1	Southern Forest Tree Improvement Committee
Pollen management	1	Southern Forest Tree Improvement Committee
Cone harvesting	1	Southern Forest Tree Improvement Committee
	GROUP D (ACTION PROGRAM LEADERS)--INDEFINITE TERMS	
Region 8, USDA Forest Service[c]	1	Regional Forester
Western Gulf Forest Tree Improvement Program	1	Director of the Cooperative
University of Florida Cooperative Forest Genetics Program	1	Director of the Cooperative
North Carolina State University-Industry Cooperative Tree Improvement Program	1	Director of the Cooperative

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[a] Membership terminates at the close of the Committee meeting in the year of expiration.

[b] As of 1982, Region 8, State and Private Forestry, USDA Forest Service, appointed by the Regional Forester.

[c] Moved from Group B to Group D in 1976.

ACCOMPLISHMENTS AND SERVICES

Subcommittees

Major subcommittees established since organization of the Committee are given in Table 2, along with dates of establishment, officers, and notes on activity. As can be seen, most of these subcommittees have been very productive.

Southwide Conferences

The committee has continued to sponsor conferences biennially (Appendix D). Attendance at conferences has increased from an average of about 90 at the first three conferences to an average of 216 at the last three. Proceedings of the Conferences likewise increased from an average of 96 pages to 276. A notable feature in recent conferences has been the inclusion of speciality workshops, such as those on cone and seed insects, pollen managment, and seed orchard yields. Distribution of Conference Proceedings has sometimes been a problem. The most recent policy (1980-81) is to print sufficient copies for free distribution to forestry school libraries and Conference registrants, plus 100 free copies for written requests. Back issues are available free from the SFTIC secretary until inventory is depleted. Requests are sent to Eastern Seed Tree Laboratory, Box 819, Macon, GA 31022. Starting with the 15th Conference, all proceedings have been submitted to the National Technical Information Service (NTIS), U.S. Department of Commerce, 5285 Port Royal Road, Springfield, Virginia 22151, for placement on microfilm and distribution. Copies can be purchased directly from NTIS.

Committee-sponsored Publications

Committee sponsored publications (1951-81) are given in Appendix E.

Newsletter

Newsletters have continued to be issued semi-annually, Beginning in 1967 the "Newsletter" was taken over by "The Pollen Grain," which was issued by Southeastern Area, State & Private Forestry (USDA-Forest Service) and the Committee. Editors were R. G. Hitt (1967-68), LeRoy Jones (1969-71), R. G. Hitt (1971-75), and Clark Lantz (1976-80). Publication of "The Pollen Grain" was suspended in December 1980, due to a federal publication moratorium.

Other Activities

1. In 1971, the Committee proposed establishment of the Seed Orchard Survey (SOS) to identify problems, research needs, and procedures for improving seed quality and yield. Findings led to providing of seed testing services by the USDA Forest Service, Eastern Tree Seed Laboratory. This service was terminated in 1975, but replaced by two new services: Seed Orchard Evaluation Testing (SOSET) and Cone Analysis Service (CAS) (Karrfalt, 1977). SOSET and CAS services were terminated in 1981.

Table 2.--Subcommittees of the Southern Forest Tree Improvement Committee.[a]

Name	Year Estab.	Chairman	Accomplishments & Status[b]
Geographic sources of seed	1951	P.C. Wakeley (1951-64) O.O. Wells (1964-).	(2, 3, 6, 10, 15, 25, 29, and 31). Wakeley (1959), Snyder et al., (1967), Wells (1969). Data tapes released 1981.
Genetic control of seed	1951	F.M. Cossitt (1951-53) T.E. Maki (1953-55) George Garin (1956-66) J.E. Barber (1966-67)	(13). Promoted seed certification. Presumably dismissed in 1967.
Tree selection and breeding	1951	K.W. Dorman (1951-68)	(4, 5, 16, and 26).
Progeny testing	1951	E.G. Wiesehuegel (1951-53)	(8). Dismissed 1953.
Tree improvement brochure	1953	D.A. Anderson and C.M. Kaufman (1953-55)	(14).
Tree improvement through silviculture	1954	E.G. Wiesehuegel (1953) Bruce Zobel (1954)	(11).
Entomology[c]	1954	R.J. Kowal (1954-64) E.P. Merkel (1964-72) H.O. Yates (1972-)	(27). Workshop held at 14th Conf. Stimulated pesticide research and clearance for use of chemicals.
Pathology[c]	1955	G.H. Hepting (1955-59) A.F. Verall (1959-64) H.R. Powers (1964-72) E.B. Cowling (1972-81) Tom Miller (1981-)	(18). Promoted establishment of fusiform rust testing lab., 1971.

Hardwood genetics	1959	H. Doyle (1959-71)	Sponsored hardwood meetings.
Progeny testing for seed certification	1960	P.C. Wakeley (1960)	(20). Dismissed 1960.
Pest handbook	1966	J.C. Barber (1966)	(27).
Orchard seed yield and quality (seed orchard survey)	1970	L. Jones (1971) R. Hitt (1971-75)	Belcher and Hitt (1973); Belcher (1974); Belcher and DeBarr (1975). Dismissed 1975.
Cone and seed insect research	1972	J. P. van Buijtenen (1972-77).	Stimulated funding. Dismissed 1977.
Gene preservation	1974	K. Taft (1974) T. Vermillion (1979-)	Inactive 1975-78. Two reports in Pollen Mgt. Hdbk. Policy statement forthcoming.
Reorganization	1976	R. Dinus (1976)	Membership structure reorganized. Dismissed 1976.
Pollen management	1977	E.C. Franklin (1977-81) F. Bridgewater (1981-)	Workshops at 14th and 15th Conf. and at Nat. Tree Seed Lab. 1980. Pollen Mgt. Hdbk., Franklin (1981).
Geographic variation in seed orchard yields	1977	Clark Lantz (1977-)	Workshop at 14th Conf. Instigated studies of geographic effects. Schmidtling (1978).
Mailing list	1977	Clark Lantz (1977-)	Mailing list placed on computer.[d]
Cone and seed harvesting	1979	S. Dianis (1979-82) J. L. McConnell (1982-)	Summary of harvest systems in use prepared.

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[a] Does not include Conference subcommittees, which are usually shown in Conference Proceedings, nominating committees, or minor temporary committees.

[b] Numbers in parentheses are Committee-sponsored publications, listed in Appendix E.

[c] Official status as subcommittee and date established are uncertain--chaired by specialists who present reports at most meetings.

[d] Most of this work was done by S. B. Land, Jr.

2. The Committee's Pathology subcommittee (E. C. Cowling, Chairman) was instrumental in developing the Resistance Screening Center in 1971 (Prior to 1980 the Center was known as the Fusiform Rust Testing Laboratory). It is operated by Region 8, State and Private Forestry, USDA Forest Service.

3. In 1973, The Southern Forest Tree Improvement Conference Committee (R. J. Dinus, Chairman, B. A. Thielges, and O. O. Wells) conducted a survey of research needs and priorities. Its report (Dinus et al., 1973) suggested a dire need for more research on cone and seed insects. This in turn resulted in establishment of the Cone and Seed Insect Research Committee (J. P. van Buijtenen, Chairman). The latter committee stimulated increased funding for research by the Southeastern Forest Experiment Station and also lobbied strongly for establishment of CSRS Regional Project S-118 dealing with seed orchard insects.

4. The Committee stimulated publication of forest tree seed orchard directories in 1971, 1974 and 1981 (USDA Forest Service, 1971, 1974 and 1982).

5. In 1977, the Committee instigated and assisted with the "Sycamore decline survey" (Progress Report in Minutes, 1977 Committee Meeting).

6. In 1981, a book on pollen management was published (Franklin ed., 1981), a major accomplishment of the Pollen Management Subcommittee.

7. Through encouragement of the Committee, a guide to cone and seed insects of southern pines was published (Ebel et al., 1980).

8. The Committee continued to promote seed certification. In a 1981 report to the Committee, Earl W. Belcher, Jr., Director of the National Tree Seed Laboratory, stated that all but three Southern States now have seed certification standards.

LITERATURE CITED

Belcher, Earl W. 1974. Observations on the third-year results of the seed orchard survey (S.O.S.). In Proc. seed yield from southern pine seed orchards, John Kraus, ed. Georgia Forest Research Council, Macon, GA.

Belcher, Earl W. and Gary L. DeBarr. 1975. Seed orchard survey (S.O.S.): final report and summary of highlights. Proc. 13th. South. For. Tree Improv. Conf.: 145-152.

Belcher, Earl W. and Robert G. Hitt. 1973. Observation on two-year results of the seed orchard survey (S.O.S.). Proc. 12th South. For. Tree Improv. Conf.: 55-63.

Dinus, R. J., B. A. Thielges, and O. O. Wells. 1973. A resume of concern from the Twelfth Southern Forest Tree Improvement Conference. Proc. 12th South. For. Tree Improv. Conf.: 348-352.

Ebel, Bernard H., Thomas H. Flavell, Loyd E. Drake, Harry O. Yates, III, and Gary L. DeBarr. Gen. Tech. Rep. SE-8, Rev., USDA, For. Service, 44p.

Franklin, E. Carlyle (ed.). 1981. Pollen management handbook. Agric. Handbk. 587. Washington, D.C.: U.S. Dep. Agric., 98 p.

Karrfalt, R. P. 1977. Seed orchard evaluation testing (SOSET) and cone analysis service (CAS) at the Eastern Tree Seed Laboratory. Proc. 14th South. For. Tree Improv. Conf.: 122-129.

Kaufman, Clemens M. 1954. The Committee on Southern Forest Tree Improvement. J. For. 52: 685-686.

Ostrom, Carl E. 1953. The activities of the Committee on Southern Forest Tree Improvement. Proc. 2nd South. Conf. For. Tree Improv.: 1-7.

Schmidtling, R. C. 1978. Southern loblolly pine seed orchards produce more cone and seed than do northern orchards. Proc. Flowering and seed development in trees 177-186: Mississippi State Univ., Starkville, MS.

Snyder, E. B., P. C. Wakeley, and O. O. Wells. 1967. Slash pine provenance tests. J. For. 65: 414-420.

USDA Forest Service. 1971. Forest tree seed orchards--a directory of industry, state, and federal forest tree seed orchards in the United States. USDA, Forest Service:15 p.

USDA Forest Service. 1974. Forest tree seed orchards. USDA Forest Service: 33 p.

USDA Forest Service. 1982. 1981 Directory of forest tree seed orchards in the United States. USDA Forest Service FS-278: 48 p.

Wakeley, P. C. 1959. Five-year results of the southwide geographic seed source study. Proc. 5th South. Conf. For. Tree Improv.: 5-11.

Wells, O. O. 1969. Results of the southwide pine seed source study through 1968-69. Proc. 10th South. Conf. For. Tree Improv.: 117-129.

Appendix A.--Membership in the Southern Forest Tree Improvement Committee, 1971-81.

Date	Name	Employer
1971-81	Julian G. Hofmann	Champion International Corp., Roanoke Rapids, NC
1971	Earl P. Stephens	U.S. Plywood-Champion Paper Inc., Pasadena, TX
1971-73	Chas. D. Webb	U.S. Plywood-Champion Paper Inc., Athens, GA
1971-74	Robert L. Koenig	Union Camp Corp., Franklin, VA
1971-75, 1977-	J. P. van Buijtenen	Texas Forest Service, College Station, TX
1971-76	C. R. Nichols, Jr.	South Carolina State Com. Forestry, Columbia, SC
1971-74	G. Y. Chamblee	North Carolina Forest Service, Raleigh, NC
1971, 1977-	Ray E. Goddard	University of Florida, Gainesville, FL
1971-77	George L. Switzer	Mississippi State University, Starkville, MS
1971-77	Eyvind Thor	University of Tennessee, Knoxville, TN
1971-72	R. W. Stonecypher	Oklahoma State University, Stillwater, OK
1971	H. L. Doyle	Hardwood Research Council, Statesville, NC
1971-77	W. A. Hubble	U.S. Plywood-Champion Paper Co., South Boston, VA
1971-79	Douglas E. Berlin	Tremont Lumber Co., Joyce, LA
1971-78	A. E. Squillace	Southeastern For. Exp. Sta., Olustee, FL
1971	D. M. Schmitt	Southern For. Exp. Sta., Gulfport, MS
1971-77	R. J. Dinus	Southern For. Exp. Sta., Gulfport, MS
1971	LeRoy Jones	SE Area, State & Private Forestry, Atlanta, GA
1971-76	R. G. Hitt	SE Area, State & Private Forestry, Atlanta, GA
1971-74	Kingsley Taft	Tennessee Valley Authority, Norris, TN
1971-74	Thomas F. Swofford	USDA Forest Service, Atlanta, GA
1971-	O. O. Wells	Southern For. Exp. Sta., Gulfport, MS
1971-72	H. R. Powers, Jr.	Southeastern For. Exp. Sta., Athens, GA
1971-72	E. P. Merkel	Southeastern For. Exp. Sta., Olustee, FL
1972-81	E. B. Cowling	N.C. State University, Raleigh, NC
1972-	H. O. Yates, III	Southeastern For. Exp. Sta., Athens, GA
1973-76	Bart A. Thielges	Louisiana State University, Baton Rouge, LA

Appendix A.--(Continued).

Date	Name	Employer
1974-81	John McCullough	Alabama Forestry Commission, Montgomery, AL
1974-81	B. W. Gibbons	Tennessee River Pulp & Paper Co., Counce, TN
1974-79	P. E. Barnett	Tennessee Valley Authority, Norris, TN
1974-	James L. McConnell	USDA Forest Service, Atlanta, GA
1974-76	Roger Blair	International Paper Co., Bainbridge, GA
1976-	Clark W. Lantz	SE Area, State & Private Forestry, Atlanta, GA
1976-79	John Stone	International Paper Co., Bainbridge, GA
1977-81	James Wynens	Georgia Forestry Commission, Macon, GA
1977-81	H. G. Harris	N.C. Dept. Nat. Resources, Raleigh, NC
1977-	P. P. Feret	V.P.I. and S. U., Blacksburg, VA
1977	Ray Hicks, Jr.	Stephen F. Austin State Univ., Nacogdoches, TX
1977-81	J. R. Toliver	Louisiana State Univ., Baton Rouge, LA
1977-	Calvin F. Bey	Southern For. Exp. Sta., Gulfport, MS
1977-81	E. C. Franklin	N.C. State University, Raleigh, NC
1977-79	B. J. Zobel	N.C. State University, Raleigh, NC
1978-	S. B. Land, Jr.	Mississippi State Univ., Mississippi State, MS
1978-	R. M. Bost	Crescent Land & Timber Corp., Charlotte, NC
1978-	J. F. Kraus	Southeastern For. Exp. Sta., Macon, GA
1979-	James Ralston	International Paper Co., Bainbridge, GA
1979-	Tom Vermillion	Crown Zellerbach Corp., Bogalusa, LA
1979-81	Dave Scanlon	Tennessee Valley Authority, Norris, TN
1979-81	Stephen Dianis	Weyerhauser Co., Plymouth, NC
1979-	Robert Weir	N.C. State University, Raleigh, NC
1981-	Dave Canavera	WESTVACO, Summerville, NC
1981-	B. D. Bongarten	University of Georgia, Athens, GA
1981-	Thomas Miller	Southeastern For. Exp. Sta., Gainesville, FL
1981-	Floyd Bridgewater	Southeastern For. Exp. Sta., Raleigh, NC

Appendix B.--Officers of the Southern Forest Tree Improvement Committee, 1951-81.

Dates	Chairman	Vice-Chairman	Secretary
1951-53	Carl Ostrom	E. G. Wiesehuegel	T. E. Bercaw
1953-55	C. M. Kaufman	G. H. Hepting	T. E. Maki
1955-57	T. E. Bercaw	E. G. Wiesehuegel	G. I. Garin
1957-59	E. G. Wiesehuegel	G. I. Garin	G. R. Condit
1959-61	G. I. Garin	G. R. Condit	B. W. Henry
1961-63	J. W. Johnson	B. W. Henry	R. A. Bonninghausen
1963-65	B. W. Henry[a]	R. A. Bonninghausen	D. E. Cole
1965-67	R. A. Bonninghausen	D. E. Cole	K. W. Dorman
1967-68	K. W. Dorman[b]	C. L. Brown[b]	R. G. Hitt[b]
1968-70	R. W. Stonecypher	J. P. van Buijtenen	K. A. Taft, Jr.
1970-72	K. A. Taft, Jr.	E. Thor	R. L. Koenig
1972-74	E. Thor	J. G. Hofmann	T. F. Swofford
1974-76	J. G. Hofmann	R. J. Dinus	C. R. Nichols, Jr.
1976-78	R. J. Dinus[c]	J. L. McConnell	P. E. Barnett
1978-80	J. L. McConnell	P. P. Feret	Clark Lantz
1980-82	P. P. Feret	S. B. Land, Jr.	H. O. Yates, III

[a] Left the Committee in 1964; term completed by A. A. Foster.

[b] Left the Committee in 1968, after serving one year.

[c] Left the Committee in 1977; term completed by J. L. McConnell.

Appendix C.--Meetings of the Southern Forest Tree Improvement Committee, 1951-81.[a]

Meeting No.	Date	Location
1	June 20, 1951	Atlanta, GA
2	Dec. 10, 1951	Biloxi, MS
3	June 3, 1952	Knoxville, TN
4	Jan. 7, 1953	Atlanta, GA
5	May 27-28, 1953	Georgetown, SC
6	Dec. 2-3, 1953	Lake City, FL
7	May 26-28, 1954	College Station, TX
8	Jan. 6-7, 1955	New Orleans, LA
9	June 7-8, 1955	Auburn, AL
10	Dec. 6-7, 1955	Gulfport, MS
11	May 22-23, 1956	Asheville, NC
12	Jan. 9, 1957	Athens, GA
13	May 21, 1957	Crossett, AR
14	May 27-28, 1958	Gainesville, FL
15	June 12, 1959	Raleigh, NC
16	Oct. 13-14, 1959	Gulfport, MS
17	May 3-4, 1960	Macon, GA
18	Oct. 13-14, 1960	Gulfport, MS
19	June 8, 1961	Gainesville, FL
20	June 13, 1962	Knoxville, TN
21	June 27, 1963	Gulfport, MS
22	June 25, 1964	Tallahassee, FL
23	June 15, 1965	Savannah, GA
24	June 16, 1966	Biloxi, MS
25	June 7, 1967	Knoxville, TN
26	June 13, 1968	Statesville, NC
27	June 16, 1969	Houston, TX
28	May 14, 1970	Raleigh, NC
29	June 14, 1971	Atlanta, GA
30	June 13, 1972	Georgetown, SC
31	June 12, 1973	Baton Rouge, LA
32	June 11-12, 1974	Knoxville, TN
33	June 9, 1975	Raleigh, NC
34	June 23, 1976	Starkville, MS
35	June 16, 1977	Gainesville, FL
36	June 13-14, 1978	Charleston, SC
37	June 14, 1979	Starkville, MS
38	June 5, 1980	College Station, TX
39	May 29, 1981	Blacksburg, VA

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[a] The 1982 meeting was held June 17, at Auburn, AL.

Appendix D.--Southern Forest Tree Improvement Conferences, 1951-81.

Conference No.	Date	Location	Hosts
1	Jan. 9-10, 1951	Atlanta, GA	Region 8, USDA Forest Service
2	Jan. 6-7, 1953	Atlanta, GA	Region 8, USDA Forest Service
3	Jan. 5-6, 1955	New Orleans, LA	South. For. Exp. Stn., USDA Forest Service
4	Jan. 8-9, 1957	Athens, GA	School of Forestry, University of Georgia
5	June 11-12, 1959	Raleigh, NC	School of Forestry, N.C. State University
6	June 7-8, 1961	Gainesville, FL	School of Forestry, University of Florida
7	June 26-27, 1963	Gulfport, MS	Institute of Forest Genetics, USDA Forest Service
8	June 16-17, 1965	Savannah, GA	Continental Can Co., and Georgia For. Res. Council
9	June 8-9, 1967	Knoxville, TN	Department of Forestry University of Tenn. and Div. of Forestry Relations Tenn. Valley Auth.
10	June 17-19, 1969	Houston, TX	Texas Forest Service
11	June 15-16, 1971	Atlanta, GA	Southeastern Area, State & Private Forestry, USDA Forest Service
12	June 12-13, 1973	Baton Rouge, LA	Louisiana State University
13	June 10-11, 1975	Raleigh, NC	N.C. State University
14	June 14-16, 1977	Gainesville, FL	University of Florida & S.E. For. Exp. Stn., USDA Forest Service
15	June 19-21, 1979	Starkville, MS	Mississippi State University
16	May 27-28, 1981	Blacksburg, VA	Virginia Polytechnic Institute and State University

Appendix E.--Publications and reports sponsored by the Southern Forest Tree Improvement Committee, 1951-1981.

1. Report of the first southern conference on forest tree improvement, held in Atlanta, Georgia, January 9-10, 1951. U. S. Forest Serv., Atlanta, Georgia, 65 pp., 1951.

2. Proposal for a cooperative study of geographic sources of southern pine seed. Subcommittee on Geographic Source of Seed. Philip C. Wakeley, Chairman. South. Forest Expt. Sta., 16 pp., illus. 1951.

3. Standardized working plan for local tests of seed source. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. South. Forest Expt. Sta., 11 pp., illus. 1951.

4. Hereditary variation as the basis for selecting superior forest trees. Subcommittee on Tree Selection and Breeding. Keith W. Dorman, Chairman. Southeast. Forest Expt. Sta., Sta. Paper 15, 88 pp. illus. 1952.

5. Directory of forest genetic activities in the South. Subcommittee on Tree Selection and Breeding, Keith W. Dorman, Chairman. Southeast. Forest Expt. Sta., Sta. Paper 17, 17 pp., 1952.

6. Working plan for cooperative study of geographic sources of southern pine seed. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. South. Forest Expt. Sta., 35 pp., illus. 1952.

7. Suggested projects in the genetic improvement of southern forest trees. Committee on Southern Forest Tree Improvement, Carl E. Ostrom, Chairman. Southeast. Forest Expt. Sta., Sta. Paper 20, 13 pp. 1952.

8. Testing tree progeny. A guide prepared by the Subcommittee on Progeny Testing, E. G. Wiesehuegel, Chairman. Tenn. Val. Authority Div. Forestry Relat. Tech. Note 14, 77 pp., illus. 1952.

9. Report of the second southern conference on forest tree improvement, Atlanta, Georgia, January 6-7, 1953. U.S. Forest Serv., Atlanta, Ga., 92 pp., illus. 1953.

10. Progress in study of pine races. Philip C. Wakeley. South. Lumberman 187(2345): 137-140, illus. December 15, 1953.

11. The role of genetics in southern forest management. Special Subcommittee of the Committee on Southern Forest Tree Improvement, Bruce Zobel, Chairman, Pt. 1, Forest Farmer 14(1):4-6, 14-15, illus. Pt. 2, Forest Farmer 14(2):8-9, 14-19, illus. Pt. 3, Forest Farmer 14(3):8-9, 14-15, illus. 1954. (Reprint, 11 pp., illus. 1954).

12. Proceedings of the third southern conference on forest tree improvement, New Orleans, Louisiana, January 5-6. 1955. South. Forest Expt. Sta., 132 pp., illus. 1955.

13. Better seed for better southern forests. Subcommittee on Genetic Control of Seed, T. E. Maki, Chairman, N. C. State Col. School of Forestry Tech. Rpt. 9, 16 pp., illus. 1955.

14. Forest tree improvement for the south. Committee on Southern Forest Tree Improvement, T. E. Bercaw, Chairman. 13 pp., illus. 1955.

15. Supplement No. 1 to the original working plan of September 12, 1952, for the southwide pine seed source study. Subcommittee on Geographic Source of Seed, Philip C. Wakeley, Chairman. South. Forest Expt. Sta., 110 pp., illus. 1956.

16. Time of flowering and seed ripening in southern pines. Subcommittee on Tree Selection and Breeding. Keith W. Dorman, Chairman, and John C. Barber. Southeast. Forest Expt. Sta., Sta. Paper 72, 15 pp., illus. 1956.

17. Proceedings of the fourth southern conference on forest tree improvement, Athens, Georgia, January 8-9, 1957. Univ. Ga., 149 pp., illus. 1957.

18. Pest occurrences in 35 of the southwide pine seed source study plantations during the first three years. B. W. Henry and G. H. Hepting. South. Forest Expt. Sta., 7 pp., illus. 1957.

19. Proceedings of the fifth southern conference on forest tree improvement, Raleigh, North Carolina, June 11-12, 1959. School of Forestry, N. C. State Col., 114 pp., illus. 1959.

20. Minimum standards for progeny-testing southern forest trees for seed-certification purposes. Subcommittee on Progeny Testing for Seed Certification Purposes. Philip C. Wakeley, Chairman. South. Forest Expt. Sta., 20 pp. 1960.

21. Proceedings of the sixth southern conference of forest tree improvement, Gainesville, Florida, June 7-8, 1961. School of Forestry, Univ. of Fla., 187 pp., illus. 1961.

22. Proceedings of a forest genetics workshop, Macon, Georgia, October 25-27, 1962. Sponsored jointly with the Tree Improvement Committee of the Society of American Foresters, and partly supported by the National Science Foundation through its grant No. GE-395. 98 pp., illus. 1963.

23. Proceedings of the seventh southern conference of forest tree improvement, Gulfport, Mississippi, June 26-27, 1963. Southern Forest Expt. Sta., Forest Service, U. S. Department of Agriculture, 74 pp., illus. 1963.

24. Proceedings of the eighth southern conference on forest tree improvement, Savannah, Georgia, June 16-17, 1965. Georgia Forest Research Council, Macon, Georgia. 1966.

25. Geographic variation in survival, growth, and fusiform rust infection of planted loblolly pine. O. O. Wells and P. C. Wakeley, Forest Science, Monograph 11, 40 pp. 1966.

26. Forest tree improvement research in the south and southeast. K. W. Dorman, U. S. Dept. of Agriculture -- Forest Service, Research Paper SE-22. 90 pp., 1966.

27. Handbook of pest identification and control in southern seed orchards and seed production areas. Committee for Southern Forest Tree Improvement, in cooperation with Southeastern Area of State and Private Forestry, U. S. Forest Service, un-paged. 1966.

28. Proceedings of the ninth southern conference on forest tree improvement, Knoxville, Tennessee, June 8-9, 1967. Dept. of Forestry, Univ. Tenn. and TVA. 138 pp., illus. 1967.

29. Variation in longleaf pine from several geographic sources; O. O. Wells and P. C. Wakeley. Forest Sci. 16:28-42. 1970.

30. Proceedings of the tenth southern conference on forest tree improvement, Houston, Texas, June 17-19, 1969. Texas Forest Service, College Station, Texas.

31. Variation in shortleaf pine from several geographical sources, O. O. Wells and P. C. Wakeley. Forest Sci. 16:415-423. 1970.

32. The Southern Forest Tree Improvement Committee, 1951-71. Kaufman, C. M. Eastern Tree Seed Laboratory, Macon, Georgia, 31 pp., illus. 1971.

33. Proceedings of the eleventh southern conference on forest tree improvement, Atlanta, Georgia, June 15-16, 1971. Eastern Tree Seed Laboratory, Macon, Georgia, 284 pp., illus. 1971.

34. Proceedings of the twelfth southern conference on forest tree improvement, Baton Rouge, Louisiana, June 12-13, 1973. Eastern Tree Seed Laboratory, Macon, Georgia, 352 pp., illus. 1973.

35. Proceedings of the thirteenth southern forest tree improvement conference, School of Forest Resources, North Carolina State University, Raleigh, North Carolina, June 10-11, 1975. Eastern Tree Seed Laboratory, Macon, Georgia, 262 pp., illus. 1975.

36. Proceedings of the fourteenth southern forest tree improvement conference, Gainesville, Florida, June 14-16, 1977. Eastern Tree Seed Laboratory, Macon, Georgia, 305 pp., illus. 1977.

37. Proceedings of the fifteenth southern forest tree improvement conference, Mississippi State University, June 19-21, 1979. Eastern Tree Seed Laboratory, Macon, Georgia, 186 pp. 1979.

38. Proceedings of the sixteenth southern forest tree improvement conference, Virginia Polytechnic Inst. and State Univ., Blacksburg, VA, May 27-28, 1981. For. Sciences Lab., USDA Forest Service, Athens, Georgia, 363 pp. 1981.

Appendix F.--Regional tree improvement committees in the U.S. and Canada (present chairmen in parentheses).

Name	Year Organized
Southern Forest Tree Improvement Committee (S. B. Land, Jr., Dept. of Forestry, P.O. Drawer FR, Mississippi State, MS 39762)	1951
Northeastern Forest Tree Improvement Committee (John A. Winieski, Box 1467, Harrisburg, PA 17120)	1953
Canadian Forest Tree Improvement Association[a/] (R. M. Rauter, Rm. 3631 Whitney Block, Queens Park, Toronto, Ontario, Canada M7A 1W3)	1973
Western Forest Genetics Association (Jack Wanek, 2600 State St., Salem, OR 97310)	1954
North Central Tree Improvement Association[b/] (Daniel Houston, Dept. of Forestry, OARDC, Wooster, Ohio 44691	1979
Rocky Mountain Forest Genetics Committee (E. Durant McArthur, 735 N. 500 East, Provo, UT 84601)	1979

[a/] Formerly, the "Committee on Forest Tree Breeding in Canada" organized in 1953, which had been reorganized from a forest tree breeding group started in 1937 in the "National Research Council" of Canada.

[b/] A merger between the former "Lake States Forest Tree Improvement Committee" organized in 1953 and the "Central States Forest Tree Improvement Committee" organized in 1958.